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Nectar intake and energy expenditure in a flower visiting bat

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Summary. In a coastal region of Venezuela the daily energy expenditure (DEE) and water turnover of the flower visiting bat *Anoura caudifer* was measured by using the doubly labeled water method. In flower visitors, this method allows independent measurement of energy intake and expenditure if the animals drink no additional water and if the nectar's energy content is known. An average DEE of 12.4 kcal/d and water exchange of 13.4 ml/d were found. Our data show a balanced energy budget when animals in the field imbibe nectar with a sugar concentration of 18–21%, which is roughly medial in the range of nectar concentrations of various bat flowers. The energy turnover of flower visiting bats is high compared with DEEs of other bat species, small mammals and birds; flower visiting bats seem to belong to those species having 'a fast spin of the life motor'.

Introduction

Flower ecosystems provide excellent models for investigating energy flow in animal populations, as the relationship between energy intake and output is particularly distinct. The pollinator's energy source, the sugar content of flower nectar, and his energy expenditure in the somewhat stereotypic and therefore clearly transparent activity of flower visiting, can both be measured relatively easily. For this reason several attempts have been made to construct quantitative energy balances for flower visiting (e.g. Wolf and Hainsworth 1971; Hainsworth 1978; Heinrich 1972).

Outside their breeding span, animals lend themselves well to such investigations, as they exist in a steady state, i.e. energy intake approximates energy output, with no energy deposit. Consequently one can assume that the amount of nectar collected is optimised in such a way that the flower visitors gather just enough energy to cover their needs for the whole 24 h day (e.g. Schuchmann and Jakob 1981), with the collecting flight itself accounting for the greatest part of the pollinator's energy output. As energy turnover depends on the distance of food sources, on nectar gain per flower in competition with other visitors, and on further parameters of the biotope, it must be measured in the field, not in the laboratory. But, due to former experimental difficulties, only very few data are known as yet on the actual energy turnover rates of various animals in their biotopes.

Development and improvement of the doubly labeled water technique (Lifson and McClintock 1966; Nagy 1980) has now overcome the difficulties and allows measurement of energy turnover in free-ranging animals. The body is injected with D_2 ^{18}O, which becomes diluted in the body water pool. The decrease of D over time enables calculation of the amount of water exchanged. From the decrease of ^{18}O beyond this reference value, the amount of CO_2 given off is then calculated. This, where *RQ* is known, gives the energy expenditure.

For flower visitors this method offers a hitherto unused possibility of control. As most nectar feeders, including flower visiting bats, usually drink no additional water, the amount of water exchanged is also a measure of nectar intake. Energy intake can then be calculated from the nectar sugar concentration. For flower visitors, therefore, the doubly labeled water method allows the determination of energy intake and expenditure independently.

Methods

Test animals and procedure

Basically the doubly labeled water technique requires measurement of reduction of D and ^{18}O in the blood over several days. For this the animals must be caught daily, but neither capture nor blood sampling should disturb their daily activity rhythm. It was therefore decided that bats for our tests should be captured in their daytime roost to give them time to calm down before they commenced their nocturnal foraging trips. Also the colony should not be too large, as the excitement in a large colony hinders recapture.

We carried out our experiments in April, 1982 in a colony of the Glossophagine bat *Anoura caudifer* (Geoffroy 1818) in the National Park Henri Pittier (Venezuela). The bats' daytime roost was in a street subway half closed with rubble. This left a concrete cavern about 10 m long and 1.7 m high, opening at one end towards a valley.

We first covered the entrance with a mist net; bats were caught in a large butterfly net, measured, weighed (beam scale, accurate to 50 mg) and individually marked with numbered plastic rings. It was not necessary to sever the antebrachial membrane if the rings were fastened close to the carpus. No irritation of the wing membrane was observed during the few days of the tests. Each animal was injected subcutaneously with ca. 100 µl of 18% (excess atom percent) oxygen-18 enriched and 10% deuterium en-

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riched H_2O. After at least one h of equilibration, 6×10 µl blood was drawn in capillary tubes from each bat before release into their roost. The capillary tubes were heat-sealed and stored, awaiting laboratory analysis.

Twenty-four hours later as many of the bats as possible were recaptured briefly for a second blood sample (6×10 µl). About 48 h after injection, recapture and blood sampling were again repeated, before the rings were removed and the bats finally freed. Additional blood samples were taken from two animals not injected, to determine the naturally occurring concentrations of D and ^{18}O in the blood. To measure dry weight, one animal was sacrificed after live weighing. Water content was found to be 70%.

Drawing blood samples

Our preliminary attempts to draw about 60 µl blood from the animals were unsuccessful. Following Baer and McLean (1972) we opened the wing vein with a stiletto. But with these tiny bats we failed to draw the required amount of blood from any test animal without puncturing both arms several times. The bats became very excited and difficult to calm; all were weakened and shocked, some to such an extent that they could not fly for some time. Obviously with this method we could not achieve the main requisite of our investigation, a minimal disturbance of activity rhythm.

Acting upon an idea of Dr. J. Núñez, we therefore developed a much more considerate technique, which has proved very valuable in the meantime in our laboratory (v. Helversen et al. in prep.). A starving Triatomid bug was placed carefully on the flight membrane of a bat, near the forearm. In our tests in Venzuela we used larvae (L 5) of *Rhodnius prolixus* from the laboratory breed of Dr. J. Núñez/IVIC. Most bugs showed interest in the victim within a few s, sought with their proboscis, usually found a larger capillary after a few puncture attempts and started sucking immediately; within about 4 min the formerly paper-thin abdomen became a plump ball. The bats meanwhile lay perfectly quiescent in our hands and seemed not even to notice the prick. When the proboscis was withdrawn no wound was left, and the puncture point was invisible.

As soon as the bug had the correct content it was removed, decapitated, the stomach was pierced and the blood drawn into glass capillary tubes. The capillar tubes need not be heparinised, as this is already effected for the experimenter by the bug. With correct choice of the larval stage 60 µl blood could easily be obtained with one bug. Resorption of water from the blood, commencing immediately, would not influence the results, as the concentration of D and ^{18}O in the sample remains unaltered. The possible thinning of blood with the bug's saliva and/or haemolymph is maximally 4%, probably very much less. Moreover, it would affect all samples about equally and therefore not change the results as D and ^{18}O turnover is calculated from concentration ratios.

Analysis of data

Analysis of the D- and ^{18}O concentrations was carried out in the Laboratory for Isotope Physics of Groningen University (Holland). Each sample was analysed in duplicate, results were averaged (mean error within samples: 3.3% for D and 1.5% for ^{18}O) and the mean values of the naturally occurring D- and ^{18}O concentrations (background level) were subtracted. The amount of water exchanged was calculated, following Lifson and McClintock (1966) as:

$$r_{H_2O}[\text{mMol/h}] = 1.04 \cdot K_{2D} \cdot N \quad (1)$$

where N is the amount of body water [mMol], and $K_{2D} = (\ln D_1 - \ln D_2)/\Delta T$ is the fractional turnover rate of the hydrogen in the body water. D_1 and D_2 are the deuterium concentrations above background level in the first and second blood sample, ΔT is the time [h] between the two samples. The production of CO_2 was calculated as:

$$r_{CO_2}[\text{mMol/h}] = \frac{N}{2.08}(K_{^{18}O} - K_{2D}) - 0.015 \cdot K_{2D} \cdot N \quad (2)$$

where $K_{2D} = (\ln {}^{18}O_1 - \ln {}^{18}O_2)/\Delta T/\cdot {}^{18}O_1$ and $^{18}O_2$ are the corresponding first and second measurements of the oxygen-18 concentrations.

Where the mean hourly energy expenditure and water turnover is not constant throughout the day and where the time interval ΔT between blood samples deviates from 24 h (or a multiple thereof), errors in the calculation of daily values will occur if the r_{H_2O} and r_{CO_2} values are multiplied by 24. In our experiments ΔT differed only slightly from full days (mean: -5.3%) and all deviations fell in the daytime resting period. As for the water exchange, it can be regarded as negligible for these deviation periods (cp. Carpenter 1969). Consequently, the daily water turnover can be calculated as

$$r^*_{H_2O}[\text{ml/d}] = r_{H_2O} \cdot \Delta T \cdot 18/1000 \quad (3)$$

with the factor 18/1000 converting mMol into ml. Total CO_2 production per day was calculated from the formula

$$r^*_{CO_2}[\text{mMol/d}] = (r_{CO_2} \cdot \Delta T + (n \cdot 24 - \Delta T) \cdot 1.88)/n \quad (4)$$

where n is the number of days between blood samples and 1.88 is the amount of CO_2 [mMol/h] produced by a resting *Anoura caudifer*. This figure is equivalent to the 0.21 kcal/h discussed on p. 182. Assuming $RQ = 1$ and 5.0 kcal/l O_2, given by the use of sugar almost exclusively, the average daily energy expenditure was calculated from $r^*_{CO_2}$ as:

$$\text{DEE [kcal/d]} = 0.0224 \cdot r^*_{CO_2} \cdot 5 \quad (5)$$

Kcal values can be converted into kJ by multiplying with 4.184.

Results

Behaviour of the bats

The daytime roost (see Methods) of the *Anoura* colony was at an altitude of ca. 450 m above sea level on the lower margin of the deciduous forest ("selva veranera") on the upper edge of the dry thornbush ("espinar"). An excellent description of the biotope is given by Schäfer (1952).

The colony consisted of 13 individuals of *Anoura caudifer*; ca. 10 *Carollia brevicauda* also inhabited the same cavern. The *A. caudifer* were all adult, 12 had red-brown fur, only one inclined to be greyer and so was possibly younger; but none had any visible epiphysial commissures. There were 9 females, 2 territorial males with large testes and 2 males without externally visible testes. No conflict was observed among the males.

All bats were awake by day, hanging from the roof,

usually singly, although sometimes small loose groups were formed. At the least disturbance they began to echolocate and then to fly around in the cavern, but they were unwilling to leave their quarters by day. The colony flew out practically as a whole soon after twilight, and most of the bats stayed out until just before dawn. Only the two territorial males returned relatively early (after 21.30–22.00 h), but probably left again several times for shorter foraging periods.

There were many flowering chiropterophilous plants close to the roost, particularly columnar cacti (*Lemaireocereus* and *Pilosocereus*) and a treelike *Capparis*. At night, in the immediate vicinity of the roost, we caught several other Glossophagine species (*Glossophaga soricina, G. longirostris* and *Anoura geoffroyi*) on *Capparis* and *Lemaireocereus*, but no *Anoura caudifer*. Thus the bats of our colony appeared to forage relatively far from their day quarters, possibly in the rain forest. This is further supported by the following observations:

(1) During the whole night females never once visited their daytime roost to rest and groom. (2) In the rainy season *A. caudifer's* daytime roosts are in the rain forest region, much higher up, and then they even forage in the mountain cloud forest, e.g. at the Portachuelo Pass, where many bats of this species were caught at an altitude of ca. 1,100 m (Ochoa 1980). (3) The single *A. caudifer* we caught foraging in April was found visiting flowers of an *Eugenia jambos* tree at ca. 800 m. In a flight cage this individual also showed perfect familiarity with blooms of *Vriesea sp.* (commonly but erroneously termed *Vriesea platynema*, v. Helversen in prep.). But this *Vriesea* bloomed only in the mountain forest around the Station of Rancho Grande (ca. 800–1,000 m). (4) Compared with other Glossophagine species, such as *Glossophaga sp., A. caudifer* has much narrower, pointed wings, and a much faster flight, perhaps adaptive for longer foraging excursions.

All things considered, the bats of the observed colony probably commute to the warmer coastal region to conserve thermoregulative energy by day, but forage by night in the higher-lying forests. In the dry season, it is very cold in the mountain forest region, temperatures can sink to less than 15° C, whereas temperatures in the day quarters were 25–27° C. Unfortunately this commuting prevents our reporting reliably on flowers visited by the colony members during the observation period.

Water exchange and energy expenditure

On 13.4.82 we caught 6 adult females from the colony, all without any external signs of gravidity; their teats were small and undeveloped. The captured animals were measured, weighed, marked and received an injection of $D_2{}^{18}O$. After blood sampling all animals were freed immediately at the roost entrance,where they flew from our hands without difficulty. Only female No. 10 left the cavern afterwards of her own accord and could not be traced, even on the following day; all the others flew up to hang from the roof, and began to preen themselves intensively. To avoid disturbances, no further checks were made that day. Night observations showed that all bats had flown out. Next day (14.4.), in a check between 09.00 and 09.40 h, besides one of the territorial males and the 5 unbanded bats, only test females Nos. 6 and 7 were found. In a search of likely spots nearby, females 8 and 11 were also caught. The bats were freed again immediately after blood sampling. On 15.4. females 7 and 8 were in the original roost, while females 10, 11 and 12 were found in quarters nearby. In this way individuals 7, 8 and 11 provided two values each (after 24 and 48 h) for the $D_2{}^{18}O$ decrease; in addition one animal (No. 6) contributed a 24 h value and two animals (Nos. 10 and 12) one 48 h value each. Results of the analysis are given in Table 1. The first seven rows comprise data for 24 h intervals, followed by two rows for 48 h intervals.

Weight checks showed no losses during the experiments (Table 1, columns b and c), indicating that nightly collecting activity was not unduly disturbed. The weight of one control animal (female No. 13), not injected and recaptured twice, also remained constant (not listed in Table 1).

All individuals gave very similar results for water turnover and energy expenditure. The average daily water intake was calculated as 13.4 ml/d (Table 1, column i; coefficient of variance $CV = 6.7\%$). The average daily energy expenditure was found to be 12.4 kcal/d (column g; $CV =$

Table 1. Energy and water turnover in *Anoura caudifer*

a	b	c	d	e	f	g	h	i	j
ring No.	W1 [g]	W2 [g]	ΔT [h]	r_{CO_2} [mMol/h]	$r^*_{CO_2}$ [mMol/d]	DEE [kcal/d]	r_{H_2O} [ml/h]	$r^*_{H_2O}$ [ml/d]	sugar [%]
6	11.5	11.5	22.2	5.28	120.6	13.5	0.63	14.0	20.5
7	11.8	11.7	23.1	5.17	121.1	13.6	0.60	13.9	20.7
	11.7	11.9	21.0	4.73	105.0	11.8	0.62	13.0	19.5
8	11.5	11.4	26.3	4.44	112.5	12.6	0.53	13.9	19.5
	11.4	11.4	18.4	4.94	101.4	11.4	0.65	12.0	20.2
11	11.7	11.3	24.8	4.64	113.6	12.7	0.58	14.4	19.1
	11.3	11.8	21.0	4.45	99.1	11.1	0.65	13.7	17.8
10	11.5	11.3	45.6	5.12	119.0	13.3	0.61	13.9	20.4
12	11.4	11.1	45.5	4.52	105.2	11.8	0.53	12.1	20.7
$\bar{x}$	11.5	11.5	–	4.82	110.8	12.4	0.60	13.4	19.8
s	0.2	0.3	–	0.33	8.4	0.9	0.05	0.9	1.0

[a] individual; [b] and [c] body weights at 1st and 2nd blood sampling; [d] time between samples; [e] CO_2 production/h, calculated from formula (2); [f] CO_2 production/d, formula (4); [g] daily energy expenditure, formula (5); [h] water turnover/h, formula (1); [i] water turnover/d, formula (3); [j] sugar concentration of nectar, for calculation see text

Table 2. Nectar concentrations of neotropical bat flowers

Species	Family	Nectar concentration [%]	*A. caudifer* known to visit	Other Glossophagines known to visit	Authors
Marcgravia myriostigma	Marcgraviaceae	9	×	×	Sazima and Sazima (1980)
Lafoensia pacari	Lythraceae	9, 13.5		×	Sazima and Sazima (1975)
Cheirostemon platanoides	Sterculiaceae	12		–	Scogin (1980)
Markea neurantha	Solanaceae	14		×	Vogel et al. (1979)
Ochroma lagopus	Bombacaceae	14		(×)	Jaeger (1974[a])
Passiflora mucronata	Passifloraceae	17 (24)		×	Sazima and Sazima (1978)
Agave palmeri	Agavaceae	17		×	Howell (1979)
Kigelia pinnata	Bignoniaceae	18.5		× [b]	Scogin (1980); Vogel (1958)
Luehea speciosa	Tiliaceae	20		×	Haber and Frankie (1982)
Eugenia jambos	Myrtaceae	24	× [c]		v. Helversen (unpubl.)
Vriesea moehringiana	Bromeliaceae	29	×	×	v. Helversen (unpubl.)
mean (range)		17 (9–29)			

[a] Jaeger (1974) investigated specimens introduced into West Africa; in South America, *Ochroma* is only exceptionally visited by Glossophagine bats (v. Helversen, unpubl.)
[b] and [c] Introduced from Africa or SE Asia into South America, where they are visited by Glossophagine bats

7.5%) – a very much higher value than has hitherto been assumed for bats.

Energy intake – a control calculation

Energy metabolism of the more highly evolved flower visiting bats derives almost exclusively from nectar. Pollen intake and occasional insects serve an additional supply of protein and are disregarded in the following calculations. The basis of the bat's metabolism can therefore be taken to be $C_6H_{12}O_6$ dissolved in water. It is most improbable, in view of the enormous amount of fluid in the nectar, that the animals drink additional water. Nectar feeding bats in the laboratory drink water only when fed extremely high sugar concentrations (over 50%).

This facilitates a control calculation for our measured energy expenditure: in equilibrium the daily amount of CO_2 produced must derive from the daily sugar intake; knowledge of the sugar concentration of the nectar allows the quantity of sugar consumed to be determined from the amount drunk. Conversely the hypothetical concentration of the nectar can be calculated from the amount drunk and the metabolic rate. If the mean metabolic rate is $r^*_{CO_2}$ [mMol CO_2/d], then the amount of sugar converted daily is $r^*_{CO_2} \cdot \frac{180}{6 \cdot 1{,}000}$ [g/d], as 1 Mol of hexose yields 6 Mols of CO_2, independent of whether glucose, fructose or sucrose is used. This value divided by the sum of sugar [g/d] and water turnover [ml/d] (Table 1, column i) allows prediction of the sugar concentration of the assimilated nectar (in weight percentage, as g sugar in g solution). Table 1, column j, gives nectar concentrations of 17.8–20.7% with a mean of 19.8%.

The calculated concentration will be too small if the bats do drink additional water, or too large if the caloric value of the pollen or insect food is at all significant. It will also be too large if not all the water has been in equilibrium with the body water pool.

A literature survey and some own measurements of nectar concentrations show that neotropic Glossophagine flowers produce a highly dilute nectar with a concentration between 9 and 29% (mean: ca. 17%) (comp. also Baker 1978). These data are summarized in Table 2. Bat flower nectar may be even slightly more dilute than hummingbird flower nectar for which Baker (1975) gave 21% as the average concentration.

The above control calculation agrees well with the expected results. Although nectar production and sugar concentration of plants can vary substantially, all test individuals gathered very similar amounts of nectar and expended very similar amounts of energy. This seems to indicate that all members of the colony collected in uniformly rich foraging grounds, perhaps even in the same area.

Discussion

Daily energy expenditure (DEE)

For calculating relations between body weight of an animal and its DEE a wide variety of different formulas has been applied in the literature (e.g. energy expressed in kJ or kcal, based on weight in g or kg, calculated from original data or their log- or ln-transformation). To simplify comparison, all formulas in the following discussion are expressed in the form $E = a\ W^b$, where W is in kg and E is in kcal/d in case of DEE but in kcal/h in all other cases.

As an estimate for the DEE of bats, Kunz (1980) gave the formula: $DEE = 184.5\ W^{0.767}$. For *A. caudifer*, with 11.5 g body weight, this produces a value of only 6.0 kcal/d. But our measured value of 12.4 kcal/d is more than twice this figure. It also exceeds the average values for other mammals, those of rodents by 37–56% ($DEE = 179.8\ W^{0.669}$, King 1974; and $DEE = 88.8\ W^{0.54}$, Grodzinski and Wunder 1975), those of insectivores by 22% ($DEE = 69.4\ W^{0.43}$, Grodzinski and Wunder 1975). We cannot yet rule out that some of these discrepancies stem from the different methods; Weathers and Nagy (1980) e.g. found that metabolism values derived from time-budgets fell 40% short of values

simultaneously measured through doubly labeled water. But it is certainly conceivable that flower visiting bats have very much higher turnover rates than terrestrial mammals and that a comparison with birds might be more appropriate. Walsberg's (1984) formula (8) $DEE = 203.6\ W^{0.605}$, derived from 42 bird species, applied to a 11.5 g *A. caudifer* predicts a value of 13.7 kcal/d, which comes close to the 12.4 kcal/d we found. The following considerations shall test whether such a high daily energy turnover is consistent with our knowledge of the gathering behaviour of small flower visiting bats.

Unfortunately all data so far reported in the literature on basal metabolic rates (BMR) and on energy expenditure in various activities must still be regarded with considerable caution (see also Kunz 1980, McNab 1982). McNab (1969) measured the BMR of *A. caudifer* and found 0.213 kcal/h, a value about twice as high as Kleiber's (1960) expectation for a mammal of that size: $BMR\ [kcal/h] = 3\ W^{0.75}$. Measurements on other Glossophagine bats gave somewhat lower, but nevertheless still high results compared with the expected values (Figs. 1 and 25 in McNab 1982). Although McNab apparently used the lowest metabolic rate of quiescent animals for his BMR values (cp. also McNab 1969), his method – designed to study the effects of ambient temperatures – suggests that he was measuring resting metabolism (RMR) in thermoneutrality rather than BMR in the post-absorptive state (cp. Grodzinski and Wunder 1975). Even a passive animal reaches BMR only after a timespan usually exceeding McNab's test periods. In fact, the RMR of an 11.5 g mammal at 25° C, calculated from interpolation between values for a 9 g and a 15 g mammal (Table 1 in Wunder 1975) yields 0.208 kcal/h, almost exactly McNab's 'BMR' value. With RMR ≈1.25 BMR (Aschoff and Pohl 1970; Kendeigh 1970; Taylor 1970; King 1974) a basal metabolism of 0.17 kcal/h appears more appropriate for *A. caudifer*. This value is similar to the 0.187 kcal/h predicted for a resting 11.5 g Passerine bird from the Aschoff and Pohl (1970) equation. It follows that an average hourly energy expenditure of 0.52 kcal/h (=12.4/24, Table 1) would amount to 3.1 BMR. This is 11% above the average 2.8 BMR of rodents (Table 4 in King 1974) and 19% above the approximate 2.6 BMR of several bird species outside the moulting and breeding periods (King 1974; Drent and Daan 1980; Weathers and Nagy 1980; Bryant and Westerterp 1980a).

From measurements undertaken with *Phyllostomus* and *Pteropus* and three bird species, Thomas (1975) produced an energy metabolism formula for an animal in horizontal flight at the most favourable speed: $P\ [kcal/h] = 50.2\ W^{0.79}$. For *A. caudifer* (11.5 g) this would mean a value of 1.48 kcal/h. But as the smallest species in Thomas' analysis had a body mass of 35 g, extrapolation of the above equation to the tiny *Anoura* is problematic. Based on the same five species Tucker (1973) produced a theory which – among other things – yields a better agreement between observed and predicted values in animals of low body mass. He arrived at $P = 55.7\ W^{0.78}$ (King's 1974 conversion), giving 1.71 kcal/h for *A. caudifer*. A very similar value (1.75 kcal/h) is predicted by Berger and Hart's (1974) independent analysis of 11 bird species, including some hovering species smaller than 10 g: $P = 45.5\ W^{0.73}$. The mean of these three values (1.65 kcal/h) will represent the minimal costs for horizontal flight in the following. For normal flight (including frequent spurts and braking, obstacle avoidance, ascent into the canopy, hovering at flowers), flight values must of course be very much higher. Even quite a small ascent (angle 2°) in Thomas' experiments with *Phyllostomus* resulted in a metabolic increase of 10%. And in budgerigars a 5° ascent led to a 6–40% increase in oxygen consumption (mean 28%), depending on the flight speed (Tucker, from King 1974). An average of 130% of the minimal value therefore appears to be reasonable, giving an estimated energy expenditure of 2.1 kcal/h in flight. This is 12.4 BMR, similar to the 12.1–14.5 kcal/h of e.g. free-ranging starlings (Westerterp and Drent 1984) and to the average 12 BMR for birds in general as predicted from the Aschoff and Pohl (1970) and Berger and Hart (1974) equations.

During the resting periods at night the animals very likely do not reach the BMR, but rather 1.7 BMR (=0.29 kcal/h), due to the energetic costs of grooming, social interactions, vocalizations and other activities (comp. King 1974; Howell 1979). Even by day the bats were not lethargic. Thus wakefulness, some activity such as grooming after release, and the specific dynamic action during digestion probably elevated the metabolic rate to 1.25 BMR (cp. Aschoff and Pohl 1970; Kendeigh 1970; Taylor et al. 1970; King 1974). With these values one can attempt to calculate how long animals must remain in flight to reach the measured 12.4 kcal/d. If 14 h are spent resting in the daytime roost, and 10 h at night are spent in activity phase, with k h in flight and (10-k) h in active resting, then:

$$2.1 \cdot k + (10\text{-}k) \cdot 0.29 + 14 \cdot 0.21 = 12.4$$

This yields a nightly flying time of 3.4 h. We consider 3–4 h per night to be perfectly realistic for the little Glossophagine bats. For the bigger *Leptonycteris* Howell (1979) estimated 3 h, and for a nectar feeding hummingbird (*Calypte anna*) Pearson (1954) recorded 2.4 h of flying, territorial disputes included. The *Anoura* of our colony very likely had less favourable collecting conditions – at least during the dry season – but costs would probably decrease in the rainy season, when journeys to the foraging grounds became shorter (see p. 180).

Of course, the hypotheses underlying these calculations are largely arbitrary, as are e.g. estimates for BMR (often confused with RMR) and for various activity costs. But unlike many other studies facing the same problems, the doubly labeled water method at least measures the total amount of expended energy, and we support our values for daily energy expenditure by comparison with energy intake values derived from the amount of nectar collected and its sugar concentration. The calculations do show that the high energy values measured in no way disagree with plausible assumptions about the animals' behaviour and with results from other species.

Problems with the water balance

According to our measurements the daily amount of water exchanged was 13.4 ml, which is about 115% of the body weight and about 165% of the body water pool. Calder and Hiebert (1983) estimated nearly the same value (120% body weight) for a 3.5 g *Selasphorus rufus* hummingbird ingesting nectar from *Ipomopsis aggregata*, the value being conjectured indirectly from the amount of energy required. Such high water intake probably occurs only in nectar feeders and some fruit eaters. The vampire bat *Desmodus rotundus* drinks a daily amount of blood which equals only 37%

(laboratory) to 50% (field) of its body weight (McFarland and Wimsatt 1969). But for *Phainopepla nitens*, a fruit eating bird with about 79% water in its diet, the doubly labeled water technique also gave a high water influx amounting to 154% of the total body water pool, with the actual figure probably being higher still (Weathers and Nagy 1980).

It cannot quite be ruled out that flower visiting bats, with their often very fluid excrements, may lose water which has not previously been in equilibrium with the body water. This would not falsify the calculation of energy expenditure, but the amount drunk daily would be set too low (comp. Weathers and Nagy 1980 for a similar argument). Then if the sugar in the gut were completely resorbed, this would also mean too high a nectar concentration in the control calculation (p. 181).

Obviously such a high water consumption jeopardizes kidney function, and above all electrolyte replacement. Even given a high evaporative loss, diuresis must still set in for some hours.

Present literature data allow only unreliable estimates of water loss through evaporation as measurements for various bat species diverge widely (comp. Carpenter 1968; Vogel 1969; Studier 1970; Howell 1976). Based on results of Carpenter (1969) for *Leptonycteris* (0.04 g H_2O/g·h in flight and 0.004 g H_2O/g·h at rest), then for flight lasting 3.5 h *A. caudifer* would evaporate ca. 2.6 g H_2O/d. The above values stem from data compiled in a much drier habitat, but if we nevertheless take them as a basis, then 10.8 g H_2O/d would have to be excreted through the kidneys. As urine flow in Glossophagine bats is minimal by day (see also Howell 1976) a maximal period of 12 h can be reckoned for excretion i.e. 1.3 ml H_2O/kg min, a rate similar to the maximum urine flow for rats produced by forcing diuresis through introduction of water into their stomachs (Heller 1956; cited from McFarland and Wimsatt 1969). In any case, the urine excreted must be extremely thin, to avoid excessive electrolyte loss. Carpenter (1959) measured 342 mosmol/kg in *Leptonycteris* (comp. Geluso 1980), by far the smallest value known so far for bats. Nectar feeders, even those living in deserts, are therefore comparable in this respect with "freshwater animals" (Calder 1981). Correspondingly, the medulla of Glossophagine kidneys seems to be very poorly developed, but little is known as yet about the renal physiology of bats (comp. e.g. Studier et al. 1983).

Flight distances and numbers of flowers visited

With an average water intake of 13.4 ml/d and a sugar concentration of 20%, the amount of nectar assimilated is 15.5 ml/d, resulting from ca. 1.08 specific weight of the sugar solution. As reported, we have unfortunately no certain information on the flowers visited by our *Anoura*, and on their nectar content; but estimates of intake rate can be made from some observations on the same-size *Glossophaga longirostris*. From one flower visit, a bat of this size will exploit an average 15–20 µl nectar. This was calculated from the mean number of *G. longirostris* visits on *Lemaireocereus griseus* flowers, and from the nectar production of covered flowers. The ca. 35 µl found by Howell (1979) for *Leptonycteris* is certainly too high for the tiny Glossophagine species, which visit the same flowers repeatedly during one night in a "trap-lining" mode.

To collect this amount of nectar an *A. caudifer* would have to perform some 800–1,000 visits nightly. Ideally, a monopoly of the nectar production of 10 Lemaireocereus flowers (ca. 1.7 ml nectar/d) or 40–50 *Vriesea moehringiana* (0.35–0.40 ml/d) would suffice. But as in fact several bats visit the same flower, they must find a corresponding multiple of flowers. Only some plants open several blooms simultaneously (e.g. *Eugenia jambos*), others open only one bloom per night (e.g. *Vriesea*). The bats may therefore have to travel quite far from flower to flower. With a total flying time of 3–4 h and 800–1,000 visits per night, visits would have to average every 11–18 s to cover the energy requirements. If a bat can visit several blooms on one plant, travelling time is a matter of seconds. But sometimes the distance between plants is 100 or 200 m or even more, which means 20–40 s travelling time at a speed of 5 m/s. Reckoning an average speed of 4 m/s, to allow for deceleration, hovering and acceleration, a bat would cover about 50 km per night – a figure showing the potential of nectar-feeding bats as long-distance pollinators. The total balance must also include quite a time for seeking new flowers. Thus the seeking and collecting schedule of a nectar-feeding bat seems to be very narrowly calculated.

The great speed and precision of a Glossophagine's approach to flowers, so fascinating for the observer in the field, and its swift flight many times in one night back and forth along much-used and refined paths, become understandable when we realize what toil Nature imposes on the flower visitors. It is only at first glance that they seem to live in a paradise where "milk and honey" flow. Although flower nectar is the food most directly meeting an animal's energy demands, flower spacing, the minute portions of nectar collected and competition with other pollinators, mainly conspecifics, make it a laborious job to fulfil the quota.

With a BMR of 1.6 times the expected one and a DEE of 3.1 BMR *A. caudifer* expends about 7 times as much energy as e.g. a sloth with a BMR of 0.4 times the expected value and a DEE of 1.8 BMR (Nagy and Montgomery 1980). Thus flower visiting bats and sloths may belong to the extremes on a scale linking the strategies of "high spin" (great agility, high energy turnover, consequently high fuel consumption) and "energetic parsimony" (miserly energy expenditure compensated by the intake of little or bad-quality fuel). Present data on other species provide little evidence that different life-form types differ consistently in their energy expenditures (see e.g. Fig. 1 in Bryant and Westerterp 1980b; formulas 9 and 10 in Walsberg 1984; but Fig. 1 in McNab 1982). Yet, based on our analysis, we suggest as a reasonable and testable hypothesis that the average daily energy expenditure may represent a characteristic feature for an animal and its ecological niche.

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