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 D₂ ¹⁸O, 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 ¹⁸O beyond this reference value, the amount of CO₂ 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 ¹⁸O 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 Glossphagine 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-
riched H₂O. After at least one h of equilibration, 6 × 10⁻¹⁰ 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 × 10⁻¹⁰ 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 ¹⁸O 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 Venezuela 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 capillary tubes need not be heparinised, as this is already effected for the experiments 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 ¹⁸O 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 ¹⁸O turnover is calculated from concentration ratios.

Analysis of data

Analysis of the D- and ¹⁸O 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 ¹⁸O) and the mean values of the naturally occurring D- and ¹⁸O concentrations (background level) were subtracted. The amount of water exchanged was calculated, following Lifson and McClintock (1966) as:

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

where N is the amount of body water [mmol], and K₂D = (ln D₁ - ln D₂)/ΔT is the fractional turnover rate of the hydrogen in the body water. D₁ and D₂ 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 CO₂ was calculated as:

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

where K₂D = (ln ¹⁸O₁ - ln ¹⁸O₂)/ΔT and ¹⁸O₁ and ¹⁸O₂ 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 rH₂O and rCO₂ 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

\[ r_{H_2O}[\text{ml/d}] = r_{H_2O} \cdot ΔT \cdot 18/1000 \] (3)

with the factor 18/1000 converting mmol into ml. Total CO₂ production per day was calculated from the formula

\[ r_{CO_2}[\text{mmol/d}] = (r_{CO_2} \cdot ΔT + (n \cdot 24 - ΔT) \cdot 1.88)/n \] (4)

where n is the number of days between blood samples and 1.88 is the amount of CO₂ [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 O₂, given by the use of sugar almost exclusively, the average daily energy expenditure was calculated from rCO₂ as:

\[ \text{DEE [kcal/d]} = 0.0224 \cdot r_{CO_2} \cdot 5 \] (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 epiphyseal 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,