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Nitrogen and energy requirements of the short-tailed fruit bat (*Carollia perspicillata*): fruit bats are not nitrogen constrained

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Abstract Nitrogen (N) and energy (E) requirements were measured in adult *Carollia perspicillata* which were fed on four experimental diets. Bats ate 1.3–1.8 times their body mass·day^{-1} and ingested 1339.5–1941.4 kJ·kg$^{-0.75}$·day^{-1}. Despite a rapid transit time, dry matter digestibility and metabolizable E coefficient were high (83.3% and 82.4%, respectively), but true N digestibility was low (67.0%). Mass change was not correlated with E intake, indicating that bats adjusted their metabolic rate to maintain constant mass. Bats were able to maintain constant mass with digestible E intake as low as 1168.7 kJ·kg$^{-0.75}$·day^{-1} or 58.6 kJ·. Metabolic fecal N and endogenous urinary N losses were 0.87 mg N·g^{-1} dry matter intake and 172.5 mg N·kg$^{-0.75}$·day^{-1}, respectively, and bats required 442 mg N·kg$^{-0.75}$·day^{-1} (total nitrogen) or 292.8 mg N·kg$^{-0.75}$·day^{-1} (truly digestible nitrogen) for N balance. Based on E and N requirements and digestibilities, it was calculated that non-reproductive fruit bats were able to meet their N requirements without resorting to folivory and without over-ingesting energy. It was demonstrated that low metabolic fecal requirements allowed bats to survive on low-N diets.

Key words Energy · Fruit bat · Nitrogen

Abbreviations *E* energy · *EUN* endogenous urinary nitrogen · *MFN* metabolic fecal nitrogen · *N* nitrogen · *MR* metabolic rate · *DMD* dry matter digestibility

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Introduction

Owing to its low nitrogen (N) content, fruit has long been considered a low-quality diet, and birds and mammals that eat only fruit are thought to have difficulty meeting their N requirements (Morton 1973; McKey 1975; Howe and Estabrook 1977; Foster 1978). Nitro limitation has been invoked to explain why (1) few bird species feed exclusively on fruit (Snow 1976, 1981; Howe and Estabrook 1977), (2) even apparently specialized frugivorous birds feed their nestlings animal tissue (Morton 1973), (3) frugivorous bats and birds have low growth rates (Snow 1962, 1971; Thomas and Marshall 1984; but Ricklefs 1976), and (4) is specialized frugivorous oilbirds (*Steatornis caripensis*) select fruit that is unusually rich in protein (Snow 1962; Thomas et al. 1993).

Thomas (1984) suggested that a fruit diet posed an additional problem in terms of the balance between energy (E) and N. He argued that because fruit has a low- N content, obligate frugivorous bats such as the pteropodids, *Epomops buettikoferi* and *Micropteropus pusillus*, are obliged to ingest large quantities of fruit to satisfy their N requirements, and in so doing they over-ingest E as an unavoidable consequence of the high E/N ratio. Thomas et al. (1993) concluded that the storage of large fat reserves during development of nestling oilbirds was consistent with this over-ingestion hypothesis.

The N-limitation in frugivorous bats is not universally accepted. Law (1992) and Kunz and Diaz (1995) argued that specialized frugivorous bats are not N-limited (and so are not forced to over-ingest E) because some species ingest N-rich supplements in the form of pollen or leaves. However, these two studies do not resolve the key problems relating to the nutrition and ecology of fruit bats and other specialized frugivores. The important question is not whether frugivorous

bats do incorporate N-rich supplements into their diet, but rather (1) are they forced to supplement their diets because they are unable to balance N requirements without an additional source of N, and (2) does the fruit intake needed to satisfy N requirements necessarily result in the over-ingestion of E?

The only studies that directly address these questions provide conflicting views. Thomas (1984) and Steller (1986) concluded that pteropodid bats could balance N requirements on an all-fruit diet, but that they were forced to over-ingest E to do so. In contrast, Herbst (1986) and Korine et al. (1996) argued that the phyllostomid bat, *Carollia perspicillata*, and the pteropodid bat, *Rousettus aegyptiacus*, could balance N requirements without incurring an over-ingestion of E on most fruits.

The difference between these studies and the major weakness in all of them lie in the fact that there are no accurate measures of urinary and fecal N losses for either pteropodid or phyllostomid bats. Urinary N and fecal N are difficult to separate in feeding trials involving fruit bats and, as a result, N requirements have been estimated from Smuts' (1935) allometric equations for EUN losses (e.g. Thomas 1984; Herbst 1986; Steller 1986; Korine et al. 1996). Fruit intake required to balance N requirements was based on crude estimates of biological value and MFN losses (e.g. Thomas 1984; Herbst 1986; Korine et al. 1996).

Predictions based on allometric equations are often in error. Thus, for non-ruminant eutherians, EUN averages 160 mg $N \cdot kg^{-0.75} \cdot day^{-1}$ as compared to Smuts' (1935) estimate of 140 mg $N \cdot kg^{-0.75} \cdot day^{-1}$, but marsupials, average EUN level is far lower (53 mg $N \cdot kg^{-0.75} \cdot day^{-1}$; Robbins 1993). Maintenance N requirements of frugivorous oilbirds (50 mg $N \cdot kg^{-0.75} \cdot day^{-1}$; Bosque and De Parra 1992) are well below the allometric predictions for birds (430 mg $N \cdot kg^{-0.75} \cdot day^{-1}$; Robbins 1993). Error in the estimation of N requirements or of required food intake would lead to false conclusions regarding the ability of fruit bats to balance their N requirements on all-fruit diets and whether the over-ingestion of E is a necessary consequence of an all-fruit diet.

The purpose of this study was to measure the digestive efficiency and E and N requirements for the frugivorous phyllostomid bat, *C. perspicillata*, and to test Thomas' (1984) prediction that frugivorous bats are forced to over-ingest E to balance their N requirements (the over-ingestion hypothesis).

Materials and methods

We conducted this study at the Biodôme de Montréal using *C. perspicillata* that had been born and raised in captivity. Prior to feeding trials bats were able to fly freely in a large cave exhibit where the ambient temperature was 23–26 °C and the light cycle was 12L:12D.

For each feeding trial, we confined five *C. perspicillata* (2–3 males and 2–3 females per trial) separately in inverted 5-l glass bottles. A wire mesh cylinder inside the bottle allowed bats to hang and climb, but not to fly. Food was presented at 1800 hours in a plastic feeder near the top of the chamber to avoid fecal contamination. Urine and feces drained through the neck into a polyethylene vial to which 1 ml of glacial acetic acid was added to avoid volatile ammonia loss. Each morning, all feces and urine were scraped from the chamber, the walls were washed with a known volume of distilled water, and the combined excreta were weighed and frozen. The bats were then weighed and transferred to a clean chamber.

Each group of five bats was presented with one of four diets of varying N and E content (Table 1). We formed the diets by adding varying amounts of high protein monkey chow (Purina 5045 25.0% crude protein) and sucrose to unsweetened canned peaches and then blending to make a uniform pure. Thus, bats were not able to eliminate the fiber portion of the fruit prior to ingestion. We designated diets according to their N and E content as low N/low E, low N/high E, high N/low E, and high N/high E. We presented bats with a given diet for a 3-day pre-trial adjustment period, and then collected feces and urine for the following 4 days. We calculated daily food intake from the mass loss of the feeder corrected for evaporative losses from a control feeder.

For analyses, excreta samples were thawed, homogenized, and subdivided into three aliquots for analyses of E, total N, and urinary N. Duplicates were run only for E. For E content, we transferred a 6-ml sample into a pre-weighed filter paper and oven-dried the combined sample at 55 °C to constant mass. We then burned the filter paper and excreta in a ballistic bomb calorimeter (Gallenkamp) and calculated the excreta E content after correcting for the E content of the filter paper. We measured the total N of the excreta in a Tecator Fiastar 5020 following digestion at 375 °C in sulphuric acid with a selenium catalyst. We estimated urinary N losses by centrifuging the sample to remove solids and successively running ammonia and urea analyses on the supernatant (Tecator 5020). Urea was transformed into ammonia by a urease digestion prior to analysis. We also measured creatinine N in a Synchron CX5 using Jaffe's kinetic method (Beckman Instruments 1989) with picric acid and a pH of 13.3. We consider that urinary N losses are the sum of ammonia, urea, and creatinine N, while fecal N is the difference between N total and urinary N.

We calculated DMD, metabolizable E coefficient, and apparent and true N digestibilities following Robbins (1993). Maintenance N requirement was estimated by regressing N balance against dietary N intake and calculating the N intake required to achieve N balance. We estimated MFN by regressing apparent N digestibility against N content of the diet, where MFN is the Y intercept. The EUN was estimated by regressing urinary N content against dietary N intake, where EUN is the Y intercept. For statistical analyses, we tested data for normality and used ANOVA when data were normal

Table 1 Composition of the four experimental diets fed to captive *Carollia perspicillata*. Diets were made up of peaches to which monkey chow and sucrose were added to adjust N and E levels. Diet compositions were based on the analysis of three samples per diet

Component	Low N/low E ($n = 3$)	Low N/high E ($n = 3$)	High N/low E ($n = 3$)	High N/high E ($n = 3$)
Dry matter ($g \cdot g^{-1}$ wet weight)	0.16	0.19	0.18	0.22
E ($kJ \cdot g^{-1}$ wet weight)	2.5	3.1	2.9	3.5
Total N ($mg \cdot g^{-1}$ wet weight	0.7	0.8	2.0	2.2

and a Kruskal-Wallis test when data were abnormally distributed. Data are presented as mean ± SE.

Results

Food and energy intake

Mass-specific food intake ($g \cdot kg^{-0.75} \cdot day^{-1}$) did not differ significantly between the four diets (Kruskal-Wallis, $H = 3.2$, $df = 3$, $P > 0.05$). Bats ingested a mean of $555.4 \pm 93.2\ g \cdot kg^{-0.75} \cdot day^{-1}$ or the equivalent of 1.3–1.8 times their body mass daily. The result of a constant food intake when dietary E content varied across the four diets was a significant difference in daily gross E intake ($H = 33.7$, $df = 3$, $P < 0.0001$). Compared with the mean intake on the low N/low E diet ($1339.5 \pm 214.2\ kJ \cdot kg^{-0.75} \cdot day^{-1}$), bats ingested 45% more E on the high N/high E diet ($1941.4 \pm 270.4\ kJ \cdot kg^{-0.75} \cdot day^{-1}$) and 24% more E on the low N/high E diet ($1662.6\ kJ \pm 288.0\ kJ \cdot kg^{-0.75} \cdot day^{-1}$).

The DMD was slightly, but significantly, lower on the high N/low E diet ($H = 27.0$, $df = 3$, $P < 0.0001$; Table 2), but this trend did not hold for the metabolizable E coefficient (ANOVA, $F = 0.8$, $df = 3$, $P > 0.05$; Table 2). Mean DMD for all diets was $83.3 \pm 6.0\%$ and the metabolizable E coefficient was $82.4 \pm 7.9\%$.

Because bats on all four diets maintained a constant metabolizable E coefficient, metabolizable E intake varied significantly between treatments ($H = 23.2$, $df = 3$, $P < 0.0001$; Table 2) and ranged from a minimum of $1168.7 \pm 201.8\ kJ \cdot kg^{-0.75} \cdot day^{-1}$ on the low N/low E diet to a maximum of $1577.3 \pm 247.9\ kJ \cdot kg^{-0.75} \cdot day^{-1}$ on the high N/high E diet.

Despite variation in E intake, mass change was not significantly related to metabolizable E intake ($r^2 = 0.0$, $df = 1.78$, $P > 0.05$; Fig. 1). Because the bats maintained a constant mass over the feeding trials, it was impossible to determine a maintenance E requirement. However, bats were able to maintain constant mass with an E intake as low as $67.2\ kJ \cdot day^{-1}$ or $1339.5\ kJ \cdot kg^{-0.75} \cdot day^{-1}$ and this can be taken as a crude estimate of the maintenance E requirement.

Nitrogen digestibility and requirement

Apparent N digestibility was significantly correlated with dietary N content ($r^2 = 0.90$, $df = 1.78$; $P < 0.001$; Fig. 2) whereby: apparent digestibility ($mg\ N \cdot g^{-1}$ dry matter intake) $= -0.87 + 0.67^*$ [N content]. The slope (0.67) estimates the mean true N digestibility while the negative intercept determines MFN at $0.873\ mg\ N \cdot g^{-1}$ dry matter intake.

The N balance was significantly related to both total dietary N intake ($r^2 = 0.89$, $df = 1.78$, $P < 0.001$; Fig. 3a) and truly digestible N intake ($r^2 = 0.97$, $df = 1.78$, $P < 0.001$; Fig. 3b). *C. perspicillata* requires a minimum intake of $442\ mg \cdot kg^{-0.75} \cdot day^{-1}$ of total N or $292.8\ mg \cdot kg^{-0.75} \cdot day^{-1}$ of truly digestible N to

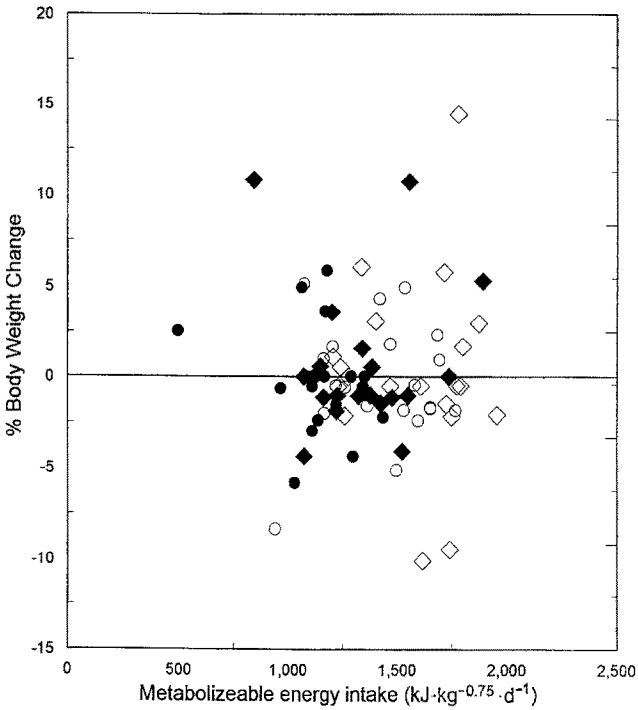

Fig. 1 Relationship between metabolizable E intake and percent change in body mass ($n = 20$ per diet). Open and filled circles indicate low N/high E and low N/low E diets, respectively. Open and filled squares indicate high N/high E and high N/low E diets, respectively

Table 2 Dry matter digestibility, metabolizable E coefficients, food intake, total E intake, metabolizable E intake for *C. perspicillata* fed four experimental diets. *P* is the probability from Anova* or Kruskal- Wallis** comparisons among groups. Diets with the same letter are not significantly different based on a Scheffé's post hoc comparison. Analyses are based on $n = 20$ per diet, representing five bats held for four days.

	Low N/low E ($n = 20$)	Low N/high E ($n = 20$)	High N/low E ($n = 20$)	High N/high E ($n = 20$)	P
Dry matter digestibility (%)	82.9 ± 7.9^a	86.4 ± 4.3^a	79.4 ± 5.6^b	84.6 ± 2.7^a	0.0001**
Metabolizable E coefficient (%)	86.9 ± 6.1^a	86.1 ± 7.0^a	75.4 ± 7.6^a	81.2 ± 5.3^a	0.475*
Food intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	535.8 ± 85.7^a	534.5 ± 92.6^a	599.6 ± 106.7^a	551.7 ± 76.8^a	0.35**
Total E intake ($kJ \cdot kg^{-0.75} \cdot day^{-1}$)	1339.5 ± 214.2^c	1662.6 ± 288.0^b	1770.8 ± 315.0^{ab}	1941.4 ± 270.4^a	0.0001**
Metabolizable E intake ($kJ \cdot kg^{-0.75} \cdot day^{-1}$)	1168.7 ± 201.8^c	1423.2 ± 235.8^{ab}	1332.1 ± 247.8^{bc}	1577.3 ± 247.9^a	0.0001**

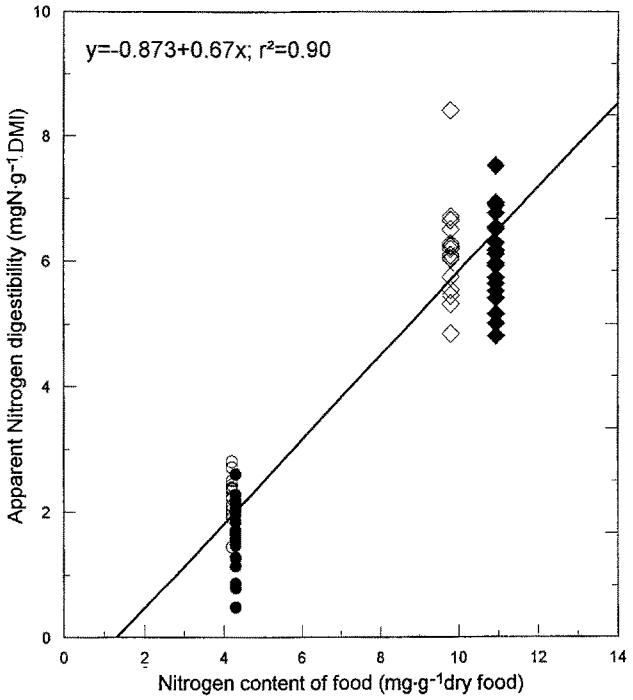

Fig. 2 Relationship between apparent N digestibility and N content of food ($n = 20$ per diet). Symbols represent the four diets as in Fig. 1

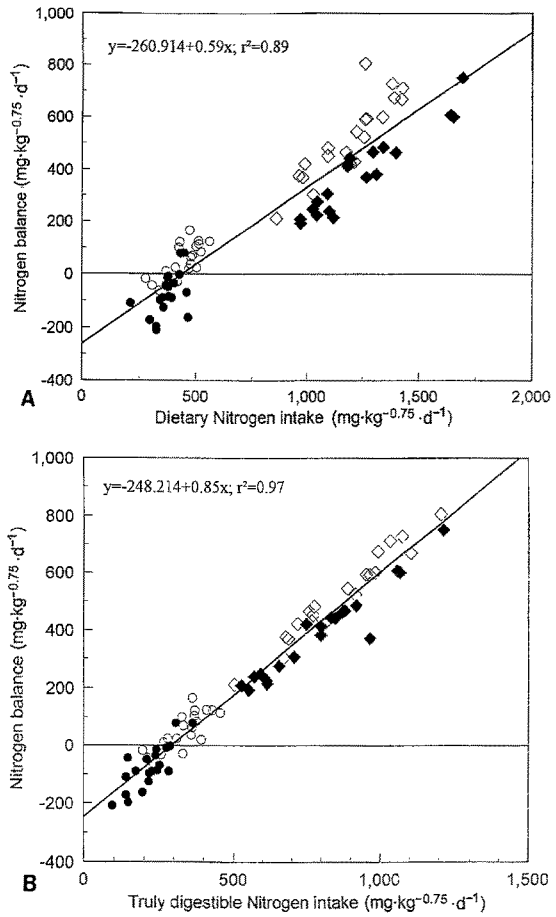

Fig. 3A, B Relationship between N balance and total dietary N intake (**A**) or truly digestible N intake (**B**) ($n = 20$ per diet). Symbols represent the 4 diets as in Fig. 1

achieve N balance. This translates to 22.2 mg · day^{-1} of total N or 14.7 mg · day^{-1} of truly digestible N for an 18.5-g individual.

Bats maintained on the high-N diets exceeded their maintenance N requirement by 33% and 77% (high N/low E and high N/high E, respectively). However, on the low-N diets, bats achieved a positive N balance on only 15 of the 20 feeding days for the low N/high E diet and only 2 of the 20 feeding days for the low N/low E diet. Figure 3A and B shows that bats fed high-E diets achieved more positive N balances than those fed low-E diets. Bats had significantly higher true N digestibilities on high-E than on low-E diets (repeated measures ANOVA: $F = 25.3$, $df = 1$, $P < 0.02$). True N digestibility was 73% on high-E diets compared with 61% on low-E diets.

Urinary N output was significantly related to dietary N intake ($r^2 = 0.31$, $df = 1.78$, $P < 0.0001$; Fig. 4) where:

$$\text{urinary N (mg} \cdot \text{day}^{-1}) = 172.5 + 0.079^* \text{ [N intake]}$$

EUN, estimated by the Y intercept, was 172.5 mg N · kg$^{-0.75}$ · day^{-1} or 8.6 mg N · day^{-1}.

Discussion

Food and energy intake and digestibility.

On the four diets, *C. perspicillata* achieved a food intake in the order of 1.3–1.8 times their body mass per day. Daily food intakes exceeding body mass appear to be the rule for frugivorous bats, having been reported for *E. buettikoferi* and *M. pusillus* (1.4–1.5, and 1.9–2.5, body mass, respectively; Thomas 1984), *R. aegyptiacus* (ca. 1, body mass; Korine *et al.* 1996), *Artibeus jamaicensis* (ca. 1, body mass; Morrison 1980) and *C. perspicillata* (0.5–1.2, body mass; Herbst 1986). Phyllostomid and pteropodid fruit bats are able to pass such large volumes of fruit through the digestive tract by having rapid gut transit times, (ca. 15–100 min; Morrison 1980; Wolton et al. 1982; Tedman and Hall 1985); however, they do not appear to sacrifice digestive efficiency greatly as a result. For *C. perspicillata* DM and metabolizable E coefficient were 83% and 82%, which are similar to values reported for pteropidid and phyllostomid species (DMD = 79–89% for *Syconycteris australis*, Law 1992; DMD = 82% for *Pteropus poliocephalus*, Steller 1986; DMD = 83% and MEC = 82% for *R. aegyptiacus*, Korine 1996; DMD = 93% and MEC = 64% for *A. jamaicensis*, Morrison 1980). Our value is substantially higher than the DM of 58% and metabolizable E coefficient of 42–48% reported by Herbst (1986), which may be explained by the fact that

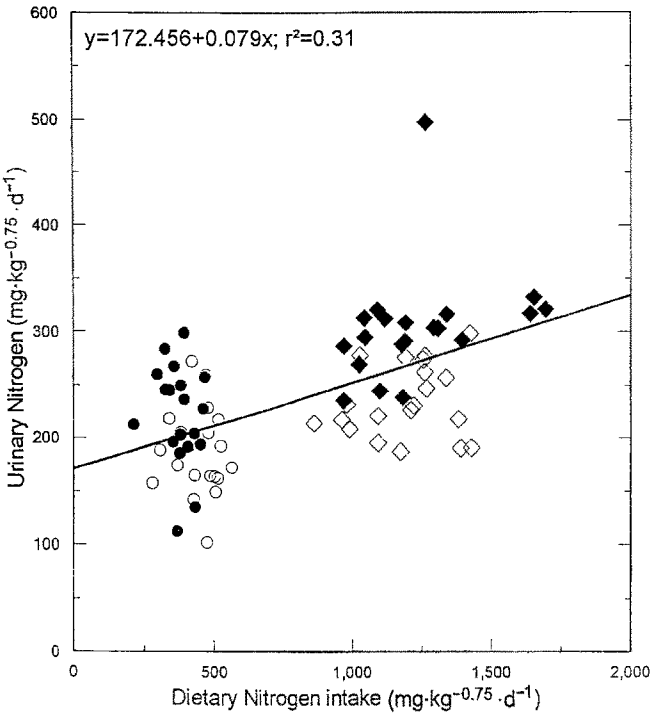

Fig. 4 Relationship between urinary N and dietary N intake ($n = 20$ per diet). Symbols represent the four diets as in Fig. 1

his bats violated the assumption of mineral balance required by his tracer method.

Frugivorous bats probably manage to maintain high DM and E digestibility despite rapid transit times because they eliminate most of the fiber portion of the fruit prior to ingestion. Thus, the swallowed juices are dominated by soluble carbohydrates that are readily absorbed in the intestine. However, true N digestibility (67% for *C. perspicillata*) is the lowest yet reported for carnivorous and herbivorous eutherians (92 ± 4.8%; Robbins 1993), suggesting that the price frugivores pay for their extremely high intake and rapid transit time is a reduced assimilation of N.

It is noteworthy that both food intake and dry matter and E digestibility remained constant through the experiments, which resulted in a highly variable E intake. Across the four diets, metabolizable E intake varied from 1168.7 to 1577.3 $kJ \cdot kg^{-0.75} \cdot day^{-1}$. If we assume that the lowest metabolizable E intake is the best approximation of a maintenance E requirement, then groups having higher intakes should have gained mass. The difference between the lowest and highest metabolizable E intake (58.6 $kJ \cdot day^{-1}$ on low N/low E vs 79.1 $kJ \cdot day^{-1}$ on high N/high E) amounts to 20.5 $kJ \cdot day^{-1}$ or the equivalent of a fat deposition of 0.5 $g \cdot day^{-1}$. Over the 7 days of feeding trials, we would have detected such a sizeable and continuous mass change, which means that bats must necessarily have adjusted E expenditures to maintain constant mass.

Such an adjustment can occur by two possible means. Animals may increase MR on high-E diets whereby excess E is radiated as heat rather than stored as fat. Changes in MR to maintain constant mass in the face of variable E intake have been described for rats and pigs and have been attributed to varying metabolic activity in the brown adipose tissue (Rothwell and Stock 1979; Gurr et al. 1980). Thomas (1984) suggested that enhanced metabolic activity in brown adipose tissue explained how *M. pusillus* and *E. buettikoferi* maintained constant mass on diets of varying E content and argued that this was an important adaptation allowing frugivores to limit E storage on E-rich but N-poor fruits. Thomas et al. (1993) also argued that high E storage (as fat deposition) in nestling oilbirds was consistent with this conclusion because birds do not possess brown adipose tissue and so cannot adjust the balance between E intake and expenditure.

Alternatively, animals may depress MR to maintain constant mass on low-E diets. Audet and Thomas (submitted) showed that *C. perspicillata* resorted to mild hypothermia when food intake was restricted and that this resulted in a significant reduction in MR. If bats were unable to increase fruit intake to meet their E requirements while maintaining elevated body temperature (normothermy) on low-E diets, then they could still maintain constant mass if they depressed their body temperature and MR to bring E expenditure into balance with intake. The fact that true N digestibility was significantly greater on high E than on low-E diets suggests that bats metabolized some protein to supplement their E intake when fed low-E diets, so reducing N retention. This is consistent with the view that the E intake on low-E diets may have been somewhat lower than that required to maintain normothermy.

Nitrogen digestibility and requirements

The combination of EUN and MFN represents the lowest rate of N loss which animals must recover through feeding if they are to maintain muscle and organ mass and body condition. It has been argued that frugivores are N-limited (e.g. Howe and Estabrook 1977) and one would then expect that selection would act to reduce one or both of these routes of N loss to the physiological minimum. The observation that oilbirds have an extremely low maintenance N requirement is viewed as an adaptation to a low-N diet (Bosque and De Parra 1992). However, our estimate of 172 mg $EUN \cdot kg^{-0.75} \cdot day^{-1}$ is slightly higher than that for non-ruminant eutherians (160 ± 22 mg $N \cdot kg^{-0.75} \cdot day^{-1}$; Robbins 1993), providing no evidence of any physiological adjustment limiting EUN losses in *C. perspicillata*.

In contrast, the MFN loss of 0.87 mg $N \cdot g\ DMI^{-1} \cdot day^{-1}$ is extremely low compared with the range of 1–9 mg $N \cdot g\ DMI^{-1}$ found for other eutherian mammals (Robbins 1993). Only the sugar glider (Smith

and Green 1987) has been reported to have a lower MFN than *C. perspicillata*, but it must be noted that no measurements of MFN have been taken for any other frugivores or nectarivores. Low MFN in frugivores and nectarivores, like *C. perspicillata* and the sugar glider, may simply reflect their lack of a functional caecum and associated intestinal flora coupled with a low-fiber fruit and nectar diet, rather than be a sign of specific physiological adjustments to low-N diets.

The levels of EUN and MFN combine to determine the maintenance N requirement which, for *C. perspicillata*, amounted to 442 mg $N \cdot kg^{-0.75} \cdot day^{-1}$. This falls within the range for eutherians (582 ± 235 mg $N \cdot kg^{-0.75} \cdot day^{-1}$; Robbins 1993), but in the upper range reported for pteropodid fruit bats (247 mg $N \cdot kg^{-0.75} \cdot day^{-1}$ for *R. aegyptiacus*, Korine 1996; 337 mg $N \cdot kg^{-0.75} \cdot day^{-1}$ for *S. australis*, Law 1992; 457 mg $N \cdot kg^{-0.75} \cdot day^{-1}$ for *P. poliocephalus*, Steller 1986). It is important to note, however, that values for maintenance N requirement are not strictly comparable between species because MFN losses depend on the dry matter content of the diet. Species feeding on low-fiber diets, such as fruit and nectar, would experience low MFN losses and hence low maintenance N requirements compared with species on high-fiber diets. Thus, one cannot argue that a low maintenance N requirement for fruit bats is evidence of a physiological adaptation to low-N diets.

Testing the over-ingestion hypothesis

Thomas (1984) argued that the fruit intake required to cover the maintenance N requirement would force bats to over-ingestion E relative to their maintenance requirement. Our data on EUN, MFN, and maintenance E requirements allowed us to test this hypothesis by calculating the intake of fruit required to satisfy N and E requirements for non-reproductive and lactating females.

Our data show that an 18.5 g non-reproductive female or male *C. perspicillata* requires 8.6 mg $N \cdot day^{-1}$ to balance EUN losses, has MFN losses of 0.87 mg $N \cdot g^{-1}$ dry matter intake, requires at least 58.6 kJ $\cdot day^{-1}$ of E, and achieves a true N digestibility of 67% and a metabolizable E coefficient of 82.4%. A female at peak lactation, producing 3.6 g milk $\cdot day^{-1}$ (Linzell 1972), would require an additional 37.7 kJ $\cdot day^{-1}$ E and 40.3 mg $N \cdot day^{-1}$ (Jenness and Studier 1976) for a total of 96.3 kJ $\cdot day^{-1}$ for maintenance E requirement and 48.9 mg $N \cdot day^{-1}$ for maintenance N requirement. We used these values to estimate the fruit intake required to supply the maintenance N requirement using the iterative procedure outlined by Mould and Robbins (1981; their Fig. 7) if bats fed on the five species of wild fruits analyzed by Herbst (1986; *Cecropia peltata*, *Chlorophora tinctoria*, *Ficus ovalis*, *Muntingia calabura*, and *Piper amalago*). If the maintenance N requirement is met before the maintenance E requirement, then bats would not be forced to over-ingest E as predicted by Thomas' (1984) over-ingestion hypothesis.

Table 3 suggests that non-reproductive individuals could satisfy their N requirements before E requirements on all fruit species. Lactating females can do so on *P. amalago* and possibly *M. calabura*, but not on *C. peltata*, *C. tinctoria*, or *F. ovalis*. We thus conclude that *C. perspicillata* is not forced to over-ingest E on the

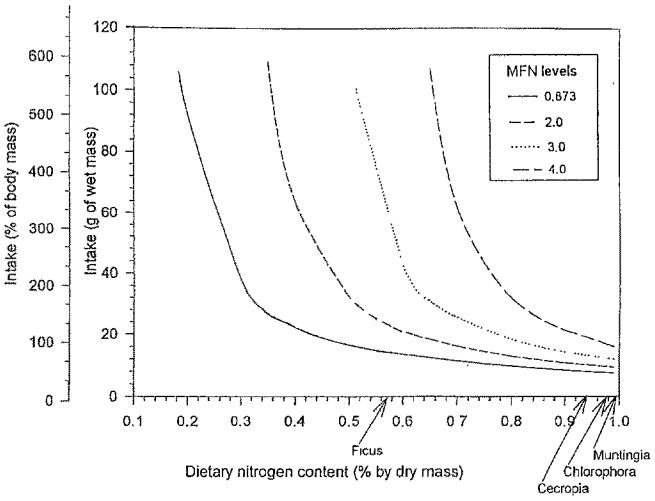

Fig. 5 Fruit intake (grams wet mass or percentage of body mass) required to achieve N balance in diets containing different levels of N depending on metabolic fecal N (*MFN*) losses. Note that as dietary N declines the required intake increases exponentially and that the size of MFN shifts these curves markedly to the right. N content of four species of fruits fed on by *C. perspicillata* and analyzed by Herbst (1986) are indicated for reference

Table 3 Estimated dry matter intake (g) of fruit required to satisfy N and E requirement of non-reproductive and lactating *C. perspicillata*. See text for the basis for calculations

Fruit species	Intake required to satisfy N		Intake required to satisfy E	
	Non-reproductive	Lactating	Non-reproductive	Lactating
Piper amalago	0.7	4.1	4.3	7.1
Ficus ovalis	2.9	16.6	4.2	6.8
Chlorophora tinctoria	1.5	8.7	4.2	6.9
Muntingia calabura	1.5	8.5	4.7	7.7
Cecropia peltata	1.6	9.0	4.4	7.2

fruits that it routinely selects. While nectarivorous bats may require an N supplement in the form of pollen as suggested by Howell (1974) and Law (1992), our analysis shows that frugivorous bats do not have to supplement their diet with N-rich sources such as leaves or pollen in order to achieve a positive N balance. When they forage on fruits to supply their E requirement, frugivorous bats ingest sufficient N to simultaneously cover their maintenance N requirement. Thus, arguments that folivory is necessary for N balance in frugivorous bats (e.g. Lowry 1989; Zortea and Mende 1993; Kunz and Diaz 1995) appear unfounded. We suggest that frugivorous bats may be seeking specific nutrients other than N through folivory (e.g. Cunningham von Someren 1972).

Fruit bats are able to subsist on diets containing as little as 0.5% N by dry mass (e.g. *Ficus* spp.; Thomas 1984, Herbst 1986) and to reproduce on diets of 1.9% N (e.g. *Piper* spp; Herbst 1986; Fleming 1988). In contrast, most other mammals require a minimum of about 1.1% N (dry mass) to achieve a positive N balance (e.g. Minson and Milford 1967; Karasov 1982; Schwartz et al. 1987; Robbins 1993). The key adaptation allowing fruit bats to exploit diets of low N content is not a reduction of EUN, but rather their low MFN losses. At 0.86 mg $N \cdot g^{-1}$ dry matter intake fruit bats fall well below the mammalian norm of about 4 mg $N \cdot g^{-1}$ dry matter intake.

To demonstrate the effect of low MFN, we calculated the minimum acceptable dietary N concentration assuming that fruit bats can ingest up to 2.5 × body mass as reported for *M. pusillus* (Thomas 1984). We then stepped MFN up from 0.86 mg $N \cdot g^{-1}$ DMI to more common mammalian values of 2.0, 3.0, and 4.0 mg $N \cdot g^{-1}$ DMI (Fig. 5). As pointed out by Mould and Robbins (1981), food intake for N balance increases exponentially as dietary N levels decline and MFN has a very large effect on the position of this curve. With their low MFN losses, fruit bats can survive (but not reproduce) on diets as low as 0.3% N by dry mass, which is well below the lowest values reported for fruits. However, at MFN losses approaching those typical of nonruminant eutherian mammals, bats would not be able to survive on succulent fruits typified by *Ficus* and they would not be able to reproduce on any fruit species.

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