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Nitrogen and Energy Balance of the Fruit Bat *Rousettus aegyptiacus* on Natural Fruit Diets

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Abstract

The nitrogen and energy balances of the Egyptian fruit bat, Rousettus aegyptiacus (Pteropodidae), were determined in a series of studies of animals on five single-fruit diets differing in their nutritional content (carob, Ceratonia siliqua; Persian lilac, Melia azedarach; loquat, Eriobotrya japonica; mulberry, Morus nigra; and sycamore, Ficus sycomorus). It was found that except for Persian lilac, these fruits, which are eaten in nature by the bats, can adequately supply their nitrogen requirements, while Persian lilac and loquat were insufficient for their energy demands. On the basis of average nutrient composition across the tested fruits, the Egyptian fruit bat (mean body mass 144 g) requires a mean intake of 6 g dry matter per day for maintaining nitrogen balance, while a mean intake of 11 g dry matter per day is needed in order to fulfill its daily energy requirements. These results suggest that energy, rather than nitrogen, is the limiting nutritional component in the diet of the fruit bat. The maintenance nitrogen requirement determined from the balance studies, $0.247 \text{ g N kg}^{-0.75} \text{ d}^{-1}$, is 55% lower than expected from allometric relations. When the lilac diet is excluded, it is even lower: $0.110 \text{ g N kg}^{-0.75} \text{ d}^{-1}$ (76% lower than expected). The maintenance nitrogen requirement is also much lower than reported for other species of fruit bats. This may reflect an adaptation to periods of low fruit availability and thus nitrogen shortage within the distribution limits of R. aegyptiacus.

Introduction

The Egyptian fruit bat, *Rousettus aegyptiacus* (Pteropodidae), is a common inhabitant of the east Mediterranean region and depends on plants as the

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main source of its diet, in the form of pollen, leaves, and mainly fleshy fruits (Kulzer 1979).

In general, fruits are characterized by high carbohydrate content and low fat and protein content (Rasweiler 1977; Mattson 1980). Thus, frugivorous species that depend on fruits as the main source of their diet may have difficulties in meeting their protein requirements.

Frugivorous birds overcome this problem by feeding on insects and seeds or selecting fruits of a relatively high protein content (Snow 1981). Neotropical frugivorous bats (Phyllostomidae) supplement their fruit diets with insects to fulfill their protein needs (Gardner 1977) or can select certain fruit species with high protein content without supplementing their diets with insects (Herbst 1986). Old World fruit bats (Pteropodidae) do not supplement their diets with insects since they lack the ability to produce ultrasonic calls (Fleming 1982). Thomas (1984) has shown that pteropodid bats may ingest up to 2.5 times their body mass in fruits per night in order to cope with their low-nitrogen fruit diets, and he also suggested that the high fruit intake of pteropodid bats is determined by the protein content of the food rather than by its energy content. Thus, pteropodid bats overingest energy to meet their nitrogen requirements. In contrast to Thomas's suggestion, Law (1992) did not find significant correlation between dry matter intake and dietary nitrogen content in artificial pollen-sugar diets consumed by the Queensland blossom bat, *Syconycteris australis* (Pteropodidae), and suggested that the high energy intake of Old World fruit bats facilitates their long-range foraging. Pteropodid bats can also supplement their low-nitrogen fruit diets by using the liquid fraction of leaves that contain high levels of nitrogen (Lowry 1989), and it has been suggested that nitrogen is not a limiting nutrient for pteropodid bats that supplement their diet with pollen (Law 1992).

Rousettus aegyptiacus is the only fruit bat out of 32 bat species in Israel. In contrast with the stable climate and the abundant food supply experienced in its global distribution, *R. aegyptiacus* in Israel faces large seasonal changes in the composition of its natural fruit diet and in fruit availability. Some of the fruits that are consumed are characterized by low protein content. However, there is no indication so far that this fruit bat supplements its diet with insects in spite of its echolocation capability (Kulzer 1979; C. Korine, personal observation).

The main question in our study was, therefore, how are the energy and nitrogen budgets of the fruit bat regulated in relation to seasonal changes in the natural diet? We also determined the maintenance nitrogen requirement from the fruit bat's natural diet and tested the general assumption that nitrogen is a limiting nutrient for pteropodid bats.

Material and Methods

Animals and Husbandry

Six adult fruit bats (three males and three nonreproductive females, 140–160 g) were captured with mist nets during the winter of 1992 in Haifa, on the northern coastal region of Israel. The bats were maintained in a temperature-controlled room ($22^{\circ} \pm 0.2^{\circ}\text{C}$, $60\% \pm 3\%$ relative humidity, 12D:12L, during all seasons). Before and between the experiments, bats were fed ad lib. with various fruits (apples, banana, etc.). Body mass was measured, and after 2–3 wk, when body mass stabilized, the feeding experiments began. The same group of bats was used in all the feeding experiments.

Fruit Diets

Preliminary field observations enabled us to define the natural fruit diets of the bats during each season. The observations were based on (1) observing at night (2–3 nights, for 4 h per night) the feeding behavior of groups of bats on various fruit plants during each season, (2) collecting spit-out remains (ejecta) and seeds from known feeding roosts and comparing them with an index of seeds in the laboratory, and (3) collecting seedless feces from day roosts and comparing them with an index of feces in the laboratory according to color and microscopic texture.

The most common fruit species that were eaten by the bats during each season and their nutritional composition are presented in Table 1. Fruits from each of these plants were picked from a single plant to reduce the variations in nutrient content among different individuals (except for Persian lilac fruits, which were collected from the same clump of plants). Fruits were collected only from plants that were visited by the bats during their night foraging. Fruits were collected seasonally in quantities needed in the feeding experiments.

Feeding Trials

The feeding experiments were carried out with a controlled, single-fruit diet (every fruit in its respective season). Each dietary experiment included an acclimation period of 8–10 d, during which body mass was measured every second or third day and during 2 additional days of adjustment to the metabolic cage. After this period the feeding experiments began.

Bats were kept overnight under husbandry conditions similar to those used during acclimation, in individual cylindrical wire cages. Each cage was placed over a plastic funnel, which drained into a glass beaker containing

TABLE 1
Fruit wet mass, nutritional composition, and water and energy content of the pulps of the different fruits

Fruit Species	Wet Mass (g)	Ash (% DM)	Nitrogen (% DM)	Crude Fat (% DM)	Carbohydrates (% DM)	Crude Fiber (% DM)	Water (% WM)	Energy (kJ/g DM)
Carob	12.1 ± 1.7	2.6	1.04	.95	82.4	7.6	20.5	16.32
Loquat	32.3 ± 5.7	4.3	.72	1.3	84.6	5.3	86.5	14.64
Mulberry	2.9 ± .9	1.0	1.08	2.9	79.9	9.4	83.9	15.89
Lilac	1.1 ± .3	6.5	1.34	2.6	70.6	10.1	15.6	16.61
Sycamore	17.6 ± 4.4	4.5	.56	2.1	84.7	5.2	83.7	15.06

Note. Fruit wet mass is given as mean ± standard deviation of 20 specimens. Other values were determined from a pooled total (all 20 specimens mashed together). DM, dry matter; WM, wet mass.

1 mL of 10% glacial acetic acid for urine collection. A wire screen was placed between the cage and the plastic funnel to separate the food remains, ejecta, and feces from the urine.

Fruits were provided *ad lib.* just before sunset on each experimental day, for 6 nights; after subtracting the uneaten remains, the daily pulp intake was calculated. Ejecta and feces were separated, collected with a spatula, and oven dried (at 60°C to constant mass) for further analysis. The 6-d collections of each individual were pooled. Efficiency of the above collection was determined by weighing the metabolic cages before the experiments and after each collection of feces, ejecta, and food remains and averaging the results ($98.12\% \pm 0.41\%$; $n = 6$). After the morning collection, the bats were returned to their original cages and the minute quantities (ca. 1% of the nightly output) of feces excreted during the day were collected before the subsequent night's experiment. These collections were pooled and analyzed separately, and the measured contents were divided and added to the night's collection for each bat.

Carob and Persian lilac are in general very dry fruits. Since they are eaten by the bats during autumn and winter, which in Israel are relatively rainy and humid, the pulp contains more water than usual. Therefore, we placed the fruits in a water bath for 24 h before feeding to obtain a similar water content to that in nature. We measured body mass changes and energy and nitrogen budgets on a carob diet without drinking water, and as a result, the bats lost, on average, 11% of their initial body mass per night, consumed less carob (60%), and could not maintain their energy balance. Therefore, the feeding experiments with carob and Persian lilac were conducted with drinking water provided *ad lib.*, and mass loss was reduced to 0.06% and 0.34% per night, respectively. Even so, one bat could not be acclimated to these diets and was therefore excluded from the analysis.

Analysis and Calculations

To measure the water content of the pulps, fruits were collected during early morning and cut within 1–2 h; the seeds were removed, and the pulps were then weighed and oven dried at 60°C to constant mass. The dry pulps were ground to powder and analyzed according to the methods of the Association of Official Analytical Chemists (1984). Ash content was determined by ignition of the dry pulp at 575°C. Nitrogen content was determined by the Kjeldahl method with a Keltec 1035 Tecator analyzer (Sweden). Crude protein was estimated as nitrogen content times 6.25. The ether extract was determined by subjecting the dry pulp to a continuous extraction with petroleum ether (40°–60°C) and ether for 4 h. Crude fiber was determined with a Fibrotec Tecator (Sweden). Nitrogen-free extractives (carbohydrates) were

calculated by subtracting the above from the total dry matter. Energy content of the dry pulp was determined in an adiabatic bomb calorimeter (Calorimeter Parr 1261). Energy contents of the oven-dried food, ejecta, and feces were determined (see above), and gross energy intake, digestible energy intake, and apparent digestibility of energy were calculated.

Daily metabolic energy requirements of all the fruit bats on all diets were determined by regressing the change in body mass on metabolizable energy intake (when the value at zero body mass change was considered to be the daily maintenance energy requirement; Robbins 1983) and assuming that the energy loss in the urine was 4% of the digestible energy intake (Grodzinski and Wunder 1975).

Nitrogen contents of the oven-dried food, ejecta, and feces were determined by the Kjeldahl method (see above). The nitrogen content of the urine was determined (every day for each bat) in an automatic analyzer (Technicon, Chem 1, United Kingdom). A complete separation of feces from urine was not possible because of the liquid nature of the feces. Therefore, the measures of urine and fecal nitrogen content were combined and presented as total nitrogen excretion. The maintenance nitrogen requirement (the amount of nitrogen intake that supports zero nitrogen balance) of the bats was calculated from the linear regression of nitrogen balance on nitrogen intake. The results are expressed on the basis of metabolic body mass ($\text{kg}^{0.75}$; Kleiber 1961). Partial apparent digestibility of nitrogen and the digestible nitrogen requirement were calculated according to Herbst (1986), with a basal metabolic rate of $0.95 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (Korine and Arad 1993).

Because of the unusual mode of eating in fruit bats, namely, ingesting fluids and leaving the fibers in the ejecta (Morrison 1980; Thomas 1984), the results of all tests can be expressed either on the basis of total consumption (total pulp intake) or on the basis of ingested pulp (total pulp intake minus spit-out pulp). The results are presented on the basis of ingested pulp.

All results are presented as means $\pm$ standard deviation. Differences among diets were tested by one-way ANOVA. Values were accepted as significant at $P < 0.05$.

Results

Our seasonal observations revealed that mainly carob (*Ceratonia siliqua*) and Persian lilac (*Melia azedarach*) are eaten during the end of autumn and during winter (82%–90% of the fecal content). Loquat (*Eriobotrya japonica*) and mulberry (*Morus nigra*) are eaten during spring and during the beginning of summer (40%–60% of the fecal content), while sycamore

(*Ficus sycomorus*) and other fig species are eaten during summer and during the beginning of autumn (75%–100% of the fecal content). There are several other fruits that are eaten by the bats in Israel, but less often. No insect remains were found in the collected feces.

In general, the fruits used in the present study (Table 1) are characterized by high water content, except for carob and Persian lilac, which are extremely dry. Carbohydrate content is relatively high in all the fruits. Lilac, mulberry, and carob were found to have relatively high crude fiber content, while in loquat and sycamore, crude fiber content was relatively low. Nitrogen and fat content vary. Sycamore has the lowest nitrogen content, while Persian lilac has the highest nitrogen content. The energy content of the pulp is similar in all fruits.

Positive correlations were found between dietary nitrogen and crude fiber ($r = 0.95$, $n = 5$ diets) and between dietary nitrogen and energy content ($r = 0.92$, $n = 5$ diets), while no such correlations were found between dietary nitrogen and fat content and between energy and fat content.

Significant differences were found in dry matter intake and the apparent digestibility of dry matter among all diets (Table 2). Of all the nutritional components, the ingested dry matter intake was significantly correlated only with carbohydrate content: dry matter intake (in g d^{-1}) = 0.46 carbohydrate content (%) – 23.88 ($n = 5$, $r = 0.89$, $F = 12.35$, $P < 0.03$).

Nitrogen balance was positive under all experimental diets, except for the lilac diet, for which it was marginally negative. An ANOVA revealed significant differences in nitrogen input and in nitrogen balance among diets (Table 2).

Body mass was maintained at relatively stable levels on all diets. After 16–18 d on any particular diet, the total change in mass ranged between 4.3% on the mulberry to –6.1% on the lilac diet (Table 2).

Total nitrogen excretion was positively correlated with the nitrogen content of fruit: nitrogen excretion (in $\text{g N kg}^{-0.75} \text{ d}^{-1}$) = 0.39 nitrogen content (%) – 0.18 ($r = 0.87$, $n = 5$, $F = 9.38$, $P < 0.05$). Nitrogen balance was significantly correlated with nitrogen intake when all diets were pooled (Fig. 1): nitrogen balance = 0.65 nitrogen intake (in $\text{g N kg}^{-0.75} \text{ d}^{-1}$) – 0.06 ($r = 0.62$, $n = 28$, $F = 16.39$, $P < 0.001$). The maintenance nitrogen requirement determined from this relationship (when the value at a nitrogen balance of zero was considered to be the maintenance requirement) was $0.247 \text{ g N kg}^{-0.75} \text{ d}^{-1}$.

A close inspection of the figure reveals that the data of the lilac diet (filled circles in Fig. 1) deviate extremely from those of the other diets. When the results of the lilac diet were excluded, the calculated maintenance nitrogen requirement was 58% lower ($0.110 \text{ g N kg}^{-0.75} \text{ d}^{-1}$): nitrogen balance = 0.82 nitrogen intake – 0.07 ($r = 0.95$, $n = 23$, $F = 191.07$, $P < 0.001$).

TABLE 2

Mean body mass changes after 16–18 d, dry matter intake, nitrogen balance, and the corresponding apparent digestibilities of the fruit bats maintained on different diets

Diet	Carob (<i>n</i> = 5)	Loquat (<i>n</i> = 6)	Mulberry (<i>n</i> = 6)	Lilac (<i>n</i> = 5)	Sycamore (<i>n</i> = 6)
Change in body mass (%)	–1.16 ^{b,c} (2.44)	–3.68 ^{c,d} (2.33)	4.30 ^a (.82)	–6.16 ^d (2.36)	.03 ^b (1.48)
Dry matter intake (g d ^{–1})	14.58 ^a (1.98)	12.99 ^b (.79)	14.31 ^{a,b} (.75)	7.76 ^c (.88)	15.37 ^a (1.12)
Apparent dry matter digestibility (%)	90.43 ^b (.71)	89.75 ^b (1.46)	88.30 ^b (2.17)	54.23 ^c (6.33)	94.21 ^a (.96)
Nitrogen intake (g N kg ^{–0.75} d ^{–1})	.54 ^a (.05)	.32 ^c (.03)	.36 ^{b,c} (.03)	.40 ^b (.05)	.13 ^d (.02)
Nitrogen excretion (g N kg ^{–0.75} d ^{–1})	.13 ^c (.009)	.13 ^c (.01)	.20 ^b (.02)	.42 ^a (.07)	.07 ^d (.007)
Nitrogen balance (g N kg ^{–0.75} d ^{–1})	.41 ^a (.04)	.19 ^b (.03)	.16 ^b (.03)	–.02 ^d (.06)	.06 ^c (.02)
Nitrogen (partial apparent digestibility corrected [%])	97.60 ^b (1.25)	97.48 ^b (2.24)	96.16 ^b (2.77)	12.53 ^c (18.32)	180.47 ^a (21.86)

Note. Results are presented as means (standard deviation); *n* indicates the number of individuals on each diet. Different superscripts in a row indicate significant differences (*P* < 0.05).

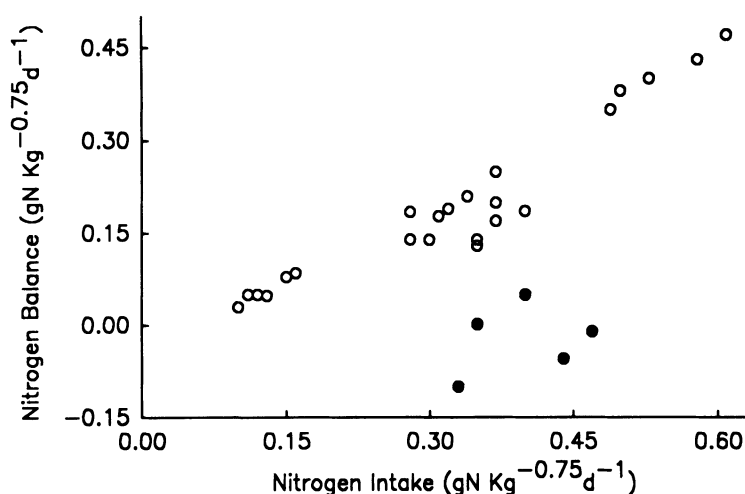


Fig. 1. The relationship between nitrogen balance and nitrogen intake in the fruit bat *Rousettus aegyptiacus* on different single-fruit diets. Filled circles represent the results on the lilac diet, and open circles represent all other diets (sycamore, loquat, mulberry, and carob).

Partial apparent digestibility was similar on carob, loquat, and mulberry diets and was extremely low on the lilac diet. The high value of partial apparent digestibility found for the sycamore diet is a result of the observed dietary nitrogen intake being lower than the expected endogenous urinary nitrogen loss (Table 2).

Nitrogen balance was significantly correlated with digestible nitrogen intake: nitrogen balance = $0.89 \text{ digestible nitrogen intake} - 0.10$ ($r = 0.94$, $n = 28$, $F = 222.7$, $P < 0.001$). The digestible nitrogen requirement determined from this relationship was $0.134 \text{ g N kg}^{-0.75} \text{ d}^{-1}$.

Significant differences were found in gross energy intake, digestible energy intake, and apparent energy digestibility among all diets (Table 3). Digestible energy intake on the lilac diet was much lower than on all other diets. The sycamore diet had the highest apparent energy digestibility, while that of the lilac diet was extremely low. This ranking is similar to that of apparent dry matter digestibility (Table 2).

Daily metabolizable energy intakes were significantly correlated with the small, yet variable, change in total body mass after 16–18 d on each diet: daily metabolizable energy intake (in kJ d^{-1}) = $0.06 \text{ total body mass change (\%)} - 10.33$ ($n = 28$, $r = 0.64$, $F = 17.69$, $P < 0.001$). The daily metabolic energy requirement determined from this relationship was 167.70 kJ d^{-1} . According to this value, loquat and lilac diets are inadequate energy sources.

TABLE 3

Gross energy intake, digestible energy intake, and apparent energy digestibility of fruit bats maintained on different diets

Diet	Gross Energy Intake (kJ d ⁻¹)	Digestible Energy Intake (kJ d ⁻¹)	Apparent Energy Digestibility (%)
Carob (<i>n</i> = 5)	220.54 ^a (27.87)	197.20 ^{a,b} (25.79)	89.26 ^b (.70)
Loquat (<i>n</i> = 6)	185.94 ^b (10.85)	164.94 ^c (7.45)	88.77 ^b (1.88)
Mulberry (<i>n</i> = 6)	218.99 ^a (16.23)	186.16 ^b (17.13)	84.99 ^c (3.01)
Lilac (<i>n</i> = 5)	122.73 ^c (14.73)	66.91 ^d (11.57)	54.38 ^d (5.64)
Sycamore (<i>n</i> = 6)	222.54 ^a (10.85)	209.04 ^a (16.43)	93.93 ^a (1.01)

Note. Results presented as means (standard deviation); *n* indicates the number of individuals on each diet. Different superscripts in a column indicate significant differences ($P < 0.05$).

Discussion

An adequate supply of nitrogen is an important factor in the ability of bats to rely on fruits as an exclusive dietary source. The present study shows that the fruit bat *Rousettus aegyptiacus* can maintain a positive nitrogen balance on a variety of natural fruit diets (except for the lilac diet, which will be discussed later). Thus, fruits can fully supply the nitrogen requirements of adult males and nonreproductive females of this species. Similar findings were reported by Herbst (1986) for the Neotropical fruit bat *Carollia perspicillata* on a diet consisting of a variety of fruits.

Thomas (1984) argued that the daily fruit intake of pteropodid bats is determined by the protein content of the food rather than by its energy content. Our findings stand in contrast with Thomas's prediction since the

only significant correlation in our study was between dry matter intake and carbohydrate content. The daily fruit consumption by *R. aegyptiacus* in the present study amounted to its body mass on the loquat, mulberry, and sycamore diets. These results are similar to the results obtained for the same species on a banana diet (Kulzer 1979). However, on carob and lilac diets the bats consumed food amounting only to approximately 0.3–0.4 of their body mass per night. The relatively low food consumption on carob and lilac diets is due to the extremely low water content of these diets, and therefore, food intake is apparently regulated on the basis of dry matter intake.

The maintenance nitrogen requirement of *R. aegyptiacus* determined in the present study was $0.247 \text{ g N kg}^{-0.75} \text{ d}^{-1}$ (all diets pooled). This can be compared with the expected maintenance nitrogen requirement by using the allometric equation of Thomas (1984) for a 144-g mammal: $(146 \text{ M}^{0.72})(1.6)(0.55 \text{ kg}^{0.75} \text{ d})^{-1}$. The value $146 \text{ M}^{0.72}$ represents endogenous nitrogen losses, where M is mass in kilograms (Maynard et al. 1979); this value is multiplied by 1.6 for nitrogen loss in the feces, which is generally 60% of the endogenous nitrogen losses for herbivores, and divided by 0.55, the biological value of plant protein (Maynard et al. 1979). The nitrogen requirement expected for a 144-g mammal as estimated from this equation is $0.450 \text{ g N kg}^{-0.75} \text{ d}^{-1}$.

The digestible maintenance nitrogen requirement of *R. aegyptiacus* was $0.134 \text{ g N kg}^{-0.75} \text{ d}^{-1}$. This can also be compared with the expected digestible maintenance nitrogen requirement from the allometric equation given by Smuts (1935): $(0.88 \text{ m}^{0.734})(6.25 \cdot 0.55 \cdot \text{kg}^{0.75} \text{ d})^{-1}$, where m is body mass, using again a biological value of plant protein of 0.55 (Maynard et al. 1979). The digestible maintenance nitrogen requirement expected for the 144-g fruit bat is $0.264 \text{ g N kg}^{-0.75} \text{ d}^{-1}$.

These results indicate that the maintenance nitrogen requirement and digestible maintenance nitrogen requirement of *R. aegyptiacus* are lower (by 55% and 51%, respectively) than predicted from allometric equations. The maintenance nitrogen requirement of *R. aegyptiacus* is also lower than measured in other pteropodid bats such as *Pteropus poliocephalus* ($0.457 \text{ g N kg}^{-0.75} \text{ d}^{-1}$; Stellar 1986) and *Syconycteris australis* ($0.337 \text{ g N kg}^{-0.75} \text{ d}^{-1}$; Law 1992) maintained on artificial diets and in the Neotropical fruit bat *Carollia perspicillata* (Phyllostomidae) ($0.263 \text{ g N kg}^{-0.75} \text{ d}^{-1}$; Herbst 1986) maintained on a variety of natural fruit diets.

Stellar (1986) pointed out that the maintenance nitrogen requirement of pteropodid bats falls within the lower range for eutherians. Our present findings show that the maintenance nitrogen requirement of *R. aegyptiacus* is the lowest found so far. In accord with the suggested coevolution between fruit bats and their plants (Heithaus 1982), we suggest that a low maintenance

nitrogen requirement developed in fruit bats as a mechanism for nitrogen conservation in the face of the low nitrogen content of their fruit diets. Since the nitrogen requirements of an animal depend on the type of food it consumes (Robbins 1983), exclusion of the low-quality lilac diet from the maintenance nitrogen requirement analysis results in an even lower than predicted maintenance nitrogen requirement (by 76%).

What may be the mechanism that permits a low maintenance nitrogen requirement in fruit bats? As presented in the introduction, fruits are characterized by high carbohydrate content and low protein content. Such a diet requires an effective regulation of glucose metabolism. A high glucose assimilation efficiency was found in *Artibeus jamaicensis* (Morrison 1980). The levels of enzymes participating in glucose metabolism in two frugivorous species were 2–3 times higher than in eight insectivorous species (Yacoe et al. 1982). Moreover, Keegan (1977) has shown that assimilation of monosaccharides in *R. aegyptiacus* was faster and greater than in the laboratory rat and concluded that the fruit bat's digestive tract is highly specialized for glucose assimilation.

Various studies have shown that glucose and insulin play important roles in body protein homeostasis by stimulating protein synthesis and decreasing protein degradation (Fukagawa et al. 1985; Florini 1987). The mechanism of action may be related to the release of insulin (Munro 1964). In response to carbohydrate absorption or infusion, insulin release increases, and this may affect protein conservation. Noncarbohydrate sources such as lactate, glycerol, and amino acids are the major precursors of glucose in the gluconeogenic pathway (Stryer 1988). The amino acids that serve as precursors for glucose can be recycled or reused for protein synthesis through the effect of insulin, which increases the turnover of glucose. It has been shown that insulin facilitates the transport of amino acids into the muscles and inhibits the release of amino acids from muscles during fasting (Pozefsky et al. 1969). A large decrease in urinary nitrogen excretion in pigs was found during infusion of glucose and insulin compared with infusion of glucose only (Fuller et al. 1977). It was also found that insulin decreases leucine flux in a dose-dependent manner in healthy postabsorptive young men because of a reduction in protein breakdown (Fukagawa et al. 1985) and that insulin decreases leucine release from liver and hind limb tissues in dogs (Abumrad et al. 1982).

The significant correlation between total nitrogen excretion and dietary nitrogen content found in the present study also suggests that nitrogen is conserved by minimizing nitrogen excretion at relatively low dietary nitrogen intakes or that it is lost when intake is high.

The low maintenance nitrogen requirement found in the fruit bat in the present study and the mechanism suggested above suggest that nitrogen

turnover may be relatively low in exclusively fruit-eating bats. Our preliminary, unpublished measurements of 3-methylhistidine (an index of muscle protein breakdown) indicate that the bats' excretion of this amino acid on the basis of metabolic body mass is relatively low ($650 \text{ nmol kg}^{-0.75} \text{ d}^{-1}$) compared with that of the laboratory rat ($6,200 \text{ nmol kg}^{-0.75} \text{ d}^{-1}$; Tomas et al. 1984). Further experiments using ^{15}N for measurement of whole-body protein turnover are needed to support the mechanism suggested above.

Low maintenance nitrogen requirements were found also in avian species that feed on low-nitrogen diets. Nitrogen balance measurements in Costa's hummingbirds (*Calypte costae*) suggest that these birds should be in balance when ingesting $72 \text{ mg N kg}^{-0.75} \text{ d}^{-1}$ (Brice and Grau 1991). Nitrogen requirements of the New Holland honeyeater (*Phylidonyris novaehollandiae*) are $60 \text{ mg N kg}^{-0.75} \text{ d}^{-1}$ (Paton 1982).

Herbivorous mammals that have adapted to arid conditions may also have low energy and nitrogen requirements (Degen and Kam 1991). Various macropodid marsupial species have different maintenance nitrogen requirements that reflect their evolutionary environments (Wallis and Hume 1992). It was found that some species that inhabit arid zones have lower maintenance nitrogen requirements than forest-inhabiting species, and the lowest value, $87 \text{ mg N kg}^{-0.75} \text{ d}^{-1}$, was measured in the sugar glider, *Petaurus breviceps* (Smith and Green 1987). In the case of *R. aegyptiacus*, a low maintenance nitrogen requirement will be adaptive in its distribution ranges, which are characterized by periods of low fruit availability and by nitrogen shortage. This is in contrast with other megachiropteran bats, whose main dietary plant materials are fruits and which are restricted to the tropical and subtropical regions of Africa, Asia, and Indo-Australia (Hill and Smith 1984), where fruits are available year-round.

Our findings show that nitrogen balance was positive under all experimental diets except for the lilac diet. A positive balance may indicate protein storage or muscle building. However, further studies are needed to evaluate the mechanisms responsible for nitrogen conservation and elucidate in which compartments and/or metabolites it is stored.

The lilac is extremely dry and has a high crude fiber content and a relatively low pulp-to-seed ratio. These traits are in contrast to traits of fruits that are generally eaten by fruit bats (Fleming 1988; Geldenhuys 1993). Yet, this fruit is one of the main fruits eaten by *R. aegyptiacus* during the winter in Israel.

The negative nitrogen and energy balance on the lilac diet results from the relatively high nitrogen excretion that is also reflected in the low values of partial apparent digestibility. This is probably due to the relatively high crude fiber content of this diet. The special mode of eating in fruit bats permits a rapid rate of food passage through the gut (30 min for *R. aegyp-*

tiacus; Keegan 1977). However, the low pulp-to-seed ratio and the relatively high fiber content of the lilac diet affects the bat's capacity for separation between the liquid and the fibers, and as a result, food passage rate is probably slow, preventing the bats from consuming more fruits in order to maintain their nitrogen and energy balance.

Another possible explanation for the negative balance on the lilac diet may be the relatively high concentrations of secondary compounds (this fruit is known to be poisonous to humans during its early ripening), which may reduce the rate of assimilation of dietary nitrogen and energy (Jakubas et al. 1993) and affect the activity of digestive enzymes (Robbins 1983).

Our experiments were carried out with single-fruit diets. In nature, the bats can switch from one species of fruit tree to a different one, as suggested by Herbst (1986), or switch to a mixed diet of leaves and fruits during their night activity in order to meet their nitrogen requirements. The collection of feces from the day roosts supported these suggestions, since we usually found between three and seven fruit species (depending on the season) in the day roost and in the night roost droppings, and remains of *Ficus* spp. leaves were observed during the winter. When we offered the bats a mixed diet of lilac fruits and leaves in the laboratory, the bats could maintain their body mass and even gain mass.

For *R. aegyptiacus*, winter is the most critical period since it is characterized by food shortage and the available fruits are of low quality. This may explain the loss in body mass and the high mortality of bats during the winter found in Makin's (1990) study. It may also explain why the main stages of reproduction (parturition and suckling) in Israel take place exclusively during spring and summer, when fruit availability and quality are high.

Is energy or nitrogen the limiting factor in the diet of *R. aegyptiacus*? Our measured minimal daily metabolizable energy requirement was 167.70 kJ d^{-1} . This is similar to the predicted value (174.15 kJ d^{-1} for a 144-g bat) for daily energy expenditure from an allometric equation derived for bats ($3.85 \text{ m}^{0.767}$, where m is body mass in grams; Kunz 1980). However, it has been suggested that this allometric equation underestimates the energy expenditure of flower-visiting bats (Helvesen and Reyer 1984). As our present value does not include the cost of flight or any social interactions, we assume that the daily energy expenditure in the field should be higher. Helvesen and Reyer (1984) suggested that comparison with a bird's daily energy expenditure might be more appropriate and used Walsberg's (1984) allometric equation ($203.6 \text{ W}^{0.605}$, where W is body mass in kilograms and daily energy expenditure is in kcal d^{-1}), to compare their results. According to Walsberg's equation, the predicted daily energy expenditure of *R. aegyptiacus* would be 263.5 kJ d^{-1} , 36% higher than presently measured in the laboratory. On the basis of the above values, an ingestion of 11–17 g

dry matter of a diet containing 0.95% N (as a percentage of dry matter) and 3.75 kcal g⁻¹ dry matter (means of the nutrient contents in the five fruits used in the present study) will be required for *R. aegyptiacus* expending energy at 167.7–263.5 kJ d⁻¹, while an ingestion of only 6 g of dry matter of the same diet will suffice to maintain nitrogen balance. These calculations are based on ingested pulp, while in reality, because of their mode of eating, the bats will consume 45% more than that (about 100% of their body mass per day). This may indicate that energy, rather than nitrogen, determines the rate of food consumption of *R. aegyptiacus* and other fruit bats, in accord with the suggestions of Law (1992) and Herbst (1986).

In summary, the fruit bat *R. aegyptiacus* can maintain its nitrogen requirements on natural fruit diets. The adaptations of a low maintenance nitrogen requirement and other traits, such as cave dwelling (Kulzer 1979), may explain why *R. aegyptiacus* is found outside the tropical and subtropical regions.

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