Dietary energy estimate inferred from fruit preferences of *Cynopterus sphinx* (Mammalia: Chiroptera: Pteropodidae) in a flight cage in tropical China

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Abstract: From a conservation standpoint, inferences about dietary intake are much more robust when placed within a demographic, temporal and nutritional context. We investigated the dietary cornerstones of fruit preference and the dietary energy gained in the Short-nosed Fruit Bat *Cynopterus sphinx*. Feeding trials were conducted with 15 wild-caught bats kept in a large flight cage in Xishuangbanna, Yunnan, China, over nine weeks. The goal was to estimate the amount of food required for the sustenance of *C. sphinx* in captivity and calculate the food amount in terms of energy. Of the fruits (apple, banana, pear, papaya and guava) offered, apple (89%) and banana (93%) were found to be preferred. The relative consumption of fruit species tended to be positively correlated with the energy value per gram fruit. Banana (93%) was the most preferred and papaya (47%) the least preferred of the offered fruits. The results suggest that the minimum recommended dietary intake is 214–267 kJ per day for an individual of *C. sphinx* in captivity with conditions allowing flight. From this, we can assume that the same energy requirements may represent the minimum intake for bats in the wild. Both body mass and food consumption decreased significantly when bats were kept in a small cage.

Keywords: Body mass, captivity, *Cynopterus sphinx,* energy intake, fruit preference.

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INTRODUCTION

Fruit bats play a crucial role in maintaining diversity in plant communities via regeneration and genetic flow of dominant forest trees (Banack 1996, 1998). Food resources like flowering and fruiting plants exert different selective forces on the foraging behaviour and energetic budgets of pollinators and the seed dispersers (Voigt et al. 2006). Fruit bats are important pollinators and seed dispersers in various ecosystems (Crome & Irvine 1986; Eby 1991; Cox et al. 1991, 1992; Elmqvist et al. 1992; Findley 1993; Rainey et al. 1995; Banack 1996, 1998). Fruit bats may feed on a large number of different fruit species and substantial dietary information is available for some *Pteropus* species (Dobat & Peikert-Holle 1985; Marshall 1985; Mickleburgh et al. 1992; Wiles & Fujita 1992). However, few studies offer a thorough investigation of the energetics of fruit bats in a single area. Theories concerning diet breadth, diet selection and the evolution of feeding strategies in frugivorous bats have been based primarily on studies of neotropical fruit-eating bats (Phyllostomidae) along with support from African fruit-eating bats (Pteropodidae) (Fleming 1982, 1986). Fleming (1986) concluded that frugivorous bats eat a taxonomically nonrandom subset of fruits and seasonal availability of fruit is a key characteristic of the fruit taxa, which has allowed bats to specialize on them. A number of different physiological and behavioural strategies have been identified in mammals helping them to accommodate increased energy demands at various stages of their life cycle. These strategies include increases in energy intake (Brody 1945; Randolph et al. 1977; Millar 1978; Hickling et al. 1991) or mobilization of fat reserves to fuel the increased demands (Fedak & Anderson 1982). Alternatively, the increased requirements at different stages can be offset by reduced physical activity (Randolph et al. 1977) or reduced maintenance energy expenditure of the mother during pregnancy (Speakman & Racey 1987). It has been shown that lactating bats *Myotis lucifugus* and *Eptesicus fuscus*) and fruit-eating megachiropteran *Rousettus aegyptiacus* increases their field metabolic rate (Korine et al. 2004; Kurta et al. 1989a)

where as the *Plecotus auritus* uses the compensatory strategies to offset increase energy demands (McLean & Speakman 1999; Voigt 2000a). Daily activity is energetically costly, and may be the reason why during resting phase *S. australis* and other blossom-bats readily enter daily torpor to reduce metabolic rate (MR) even under mild environmental conditions (Bartholomew et al. 1970; Kulzer & Storf 1980; Geiser et al. 1996; Coburn & Geiser 1996, 1998; Bonaccorso & McNab 1997; Bartels et al. 1998; Geiser 1998). Energy expenditure in the field can differ substantially from that predicted from basal metabolic rate (BMR) measurements in the laboratory (Geiser & Coburn 1999).

As a group, bats have several characteristics unique among mammals with respect to their energy allocation and life histories. They are typified by having long life spans for their body sizes, and most species give birth to a single offspring followed by an extended parental care period (Kunz & Pierson 1994). Moreover, pups do not begin foraging independently until they have nearly achieved adult size, possibly due to the constraints of flight (Barclay 1994).

Energy consumption and expenditure have been studied mainly in insectivorous free-ranging microchiropterans (Kunz 1974; Speakman & Racey 1987; Kurta et al. 1989a,b, 1990; Kunz et al. 1995; Stern et al. 1997; McLean & Speakman 1999; Reynolds & Kunz 2000) and a few on fruit eating bats (Thomas 1984; Korine et al. 2004; Voigt et al. 2006). One may expect significant differences between the insectivorous microchiropterans and the frugivorous megachiropterans because of the latter's generally larger size and fruit-based diet. Proteins have sometimes been considered a limiting nutrient for frugivorous bats, as fruits are generally low in nitrogen (Thomas 1984; Courts 1998, Elangovan & Marimuthu 2001). Thomas (1984) hypothesized that many frugivorous bat species over-ingest fruits to obtain sufficient protein with their diets. This may be the reason why many species of flying foxes also use flowers and leaves (Marshall 1985), as both flowers and leaves can contain substantial amounts of protein (Law 1992; Kunz & Diaz 1995; Ruby et al. 2000). A number of dietary studies provide lists or tabulations of dietary items used by flying foxes, but quantifications of the amount of food intake are missing (e.g., Ratcliffe 1932; Funmilayo 1979; Dobat & Peikert-Holle 1985; Marshall 1985; Richards 1990; Fujita 1991; Mickleburgh et al. 1992; Widmann 1996; Entwistle & Corp 1997; Eby 1998). However, Elangovan & Marimuthu (2001) reported the dietary intake and specifically the nitrogen content in the diet of *C. sphinx*. From a conservation standpoint, inferences about dietary intake are much more robust when placed within a demographic, temporal, and nutritional context.

We investigated the dietary cornerstones of (i) the food preference, and (ii) the respective energy gained based on results obtained with 15 wild-caught specimens of the Indian Short-nosed Fruit Bat (*C. sphinx*). *C. sphinx* feeds mainly on fleshy-pulpy fruits growing in and around the tropical rainforest, and also visits fruit orchards and exploit seasonally available fruits. This study aimed at (i) estimating the amount of food required for the sustenance of *C. sphinx* in captivity, and (ii) to calculate the food amount in terms of energy intake. In addition, we tested the hypothesis that of the above-mentioned three main strategies used by small mammals to cope with the energetic demands, *C. sphinx* would rather decrease food consumption in proportion to cage size. While the study estimates the food requirements to conserve or keep bats in captivity, the average dietary intake in captivity may also mark the minimum requirement of the species in the wild.

METHODS

Bat collection and maintenance in captivity

Eleven male and four female Indian Short-nosed Fruit Bats were mist netted in their natural habitats in and around Xishuangbanna Tropical Botanical Garden (21^{0}55.60'N & 101^{0}15.94'E), in southern Yunnan Province, southwestern China. The bats (n = 15) were accommodated and kept in a newly set up flight cage for nine weeks. Thereafter the bats (n = 6) were individually housed for four weeks in small wire mesh cages, where their flights were confined to the cage. All bats were released at the end of the investigation.

Enclosure design and the captive environment govern a variety of behaviours that captive bats display (Heard 1998; Wilson 1988). Since bats are the only group of mammals that can truly fly, they need special attention as flight is severely limited in captivity (Wilson 1988). Greenhall (1976) suggested for experiments that cage sizes should be such that the bat can fly freely or not at all. For our study we used both a flight cage and subsequently a set of flight-restricting cages. The flight cage had a dimension of 10 x 5 x 2.5 m, which allowed the bats to fly and dispose extra fat. The flight cage was set up under the canopy of a 50 year old rubber tree plantation to provide a mild climate and avoid extreme day and night temperatures. For the second set of feeding experiments, the bats were transferred to smaller wire-mesh cages (52 x 26 x 30 cm), which absolutely limited the flight option and made the bats more sedentary.

Feeding trials

To evaluate the food requirements, bats were kept in two different captive conditions and feeding trials were conducted over a period of two months in the flight cage and for one month in the flight restricted cage. The whole experiment was based on a natural fruit diet and the feeding trials were based on five different fruits. Of the five species of fruit, randomly three fruit species were display

in 12 hanging food cups in different combination each day. To ensure fruit preference was unbiased, all possible combinations were tested for the five fruit species. Each fruit type was weighed separately using a digital balance (Scout™ Pro-balance, Ohaus Corporation, USA; precision of 0.5g) before given to the bats. The following evening the remaining fruits were collected separately by species in plastic bags, and weighed. Approximately 100g fruit per bat were provided each day prior to sunset. Water was given ad libitum. Prior to the experiment, the fruits were cut into similar size and displayed to account for the water loss due to evaporation. We found negligible water loss due to very high humidity and tropical climate of the study area. The food preference was inferred from the difference between the amount of fruit offered and consumed. In order to verify a possible change in consumption, the amount of fruit displaced remained the same in both the captive conditions. The bats were re-trapped and weighed to record the change in the body mass each weekend, which indirectly infers the estimated fat accumulation. Conversion from fruit intake to energy content and nutritional values were derived based on Smolin & Grosvenor (1994) and compared with FAO (1995) as well as Centre for Food Safety Hong Kong (2006), The standard energy values per gram of fruits were taken and multiplied by the actual amount of food intake by the bats in our experiment. Following Duncan & Young (2002) the selectivity index (S.I.) for each fruit type was calculated as

$$\text{S.I.} = \frac{(1/3 - P_i)^2 + (1/3 - P_j)^2 + (1/3 - P_k)^2}{2/3}$$

where P_i, P_j and P_k are the proportions of the foods consumed per day.

RESULTS

Fruit preference

Three combinations of fruit offers including three to four different fruits were tested to examine food preferences in *C. sphinx*. Three Combined offers included both tropical fruits, which were available in abundance for the local bat population such as banana (B), guava (G), and papaya (PA), and fruits like apple (A) and pear (PE), which are not native and only available from few orchards within the region. From the combined offers of apple, banana, pear, and guava, the bats preferred apple and banana *(x^2 = 15.08, df = 3, p < 0.05)* (and reconfirmed performing Wilcoxon signed ranks test, z = 2.275, p = 0.028). The selectivity index for apple was 0.43, banana 0.39, pear 0.13, guava 0.11 and papaya 0.07 (Fig. 1). The same fruits were preferred when combined with papaya, and the preference for apple also dominated over guava and pear (two-tailed Mann–Whitney U-test, U = 0, $N_1 = N_2 = 6$, p < 0.03). The offer of banana, apple and papaya in a percentage proportion of roughly 40:20:40 resulted in a predominant consumption of banana (two-tailed Wilcoxon signed-ranks test, t = 0, N = 10, p < 0.03). Papayas yield the lowest preference (sign test; $x = 1$, N = 10, p < 0.04) amongst both the native and uncommon fruits. The relative consumption of fruit species, i.e., (fruit X consumed / fruit X offered)*100, tended to be positively correlated (r = 0.82) with the caloric value per gram fruit (Fig. 2) based

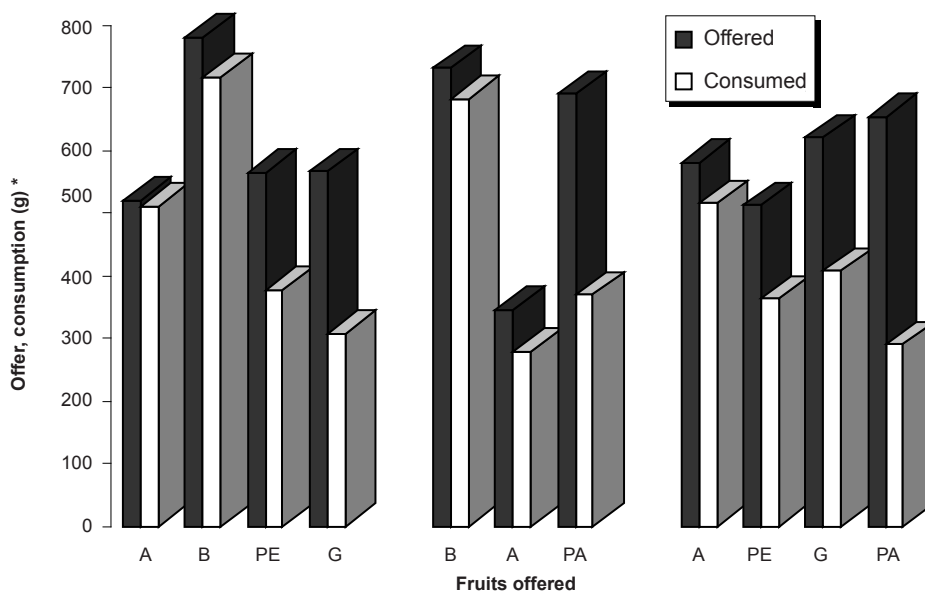**Figure 1. Fruit offer and fruit consumption of *C. sphinx* (n = 15) during two months in captivity.**
* - Three combinations of five different fruit offered; A - Apple; B - Banana; PE - Pear; G - Guava; PA - Papaya
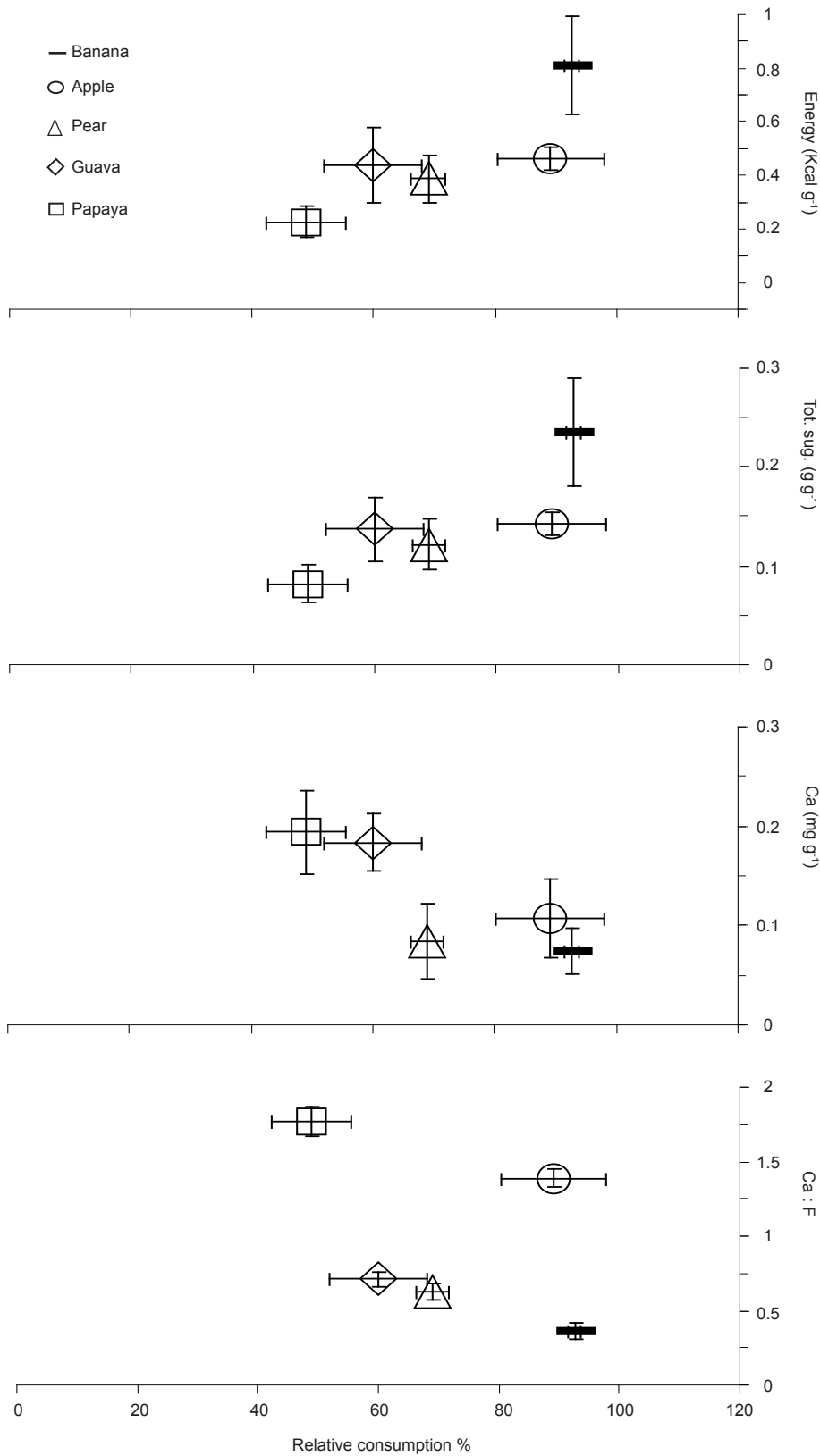
Figure 2. **Nutritional values of fruit species versus the relative consumption by *C. sphinx* in captivity.**
Consumption of fruits shows the trend to correlate with both energy- and total sugar content.

on averages derived from three independent sources (Smolin & Grosvenor 1994; FAO 1995; Center for Food Safety Hong Kong 2006). Mainly apple escaped the trend. Contrasting, both the calcium content and the calcium-to-phosphorus ratio were rather negatively correlated with the food preference of the bats during the experimental period (cold season).

Fruit consumption

The fruit consumption was significantly lower during the first two days compared to the rest of captive period ($x^2 = 21.5$, df = 4, p < 0.05; Fig. 3). The consumption was steady (73–74%) and did not differ significantly during the initial five weeks (two-tailed Wilcoxon signed-ranked tests; p > 0.3). The consumption showed an increment by
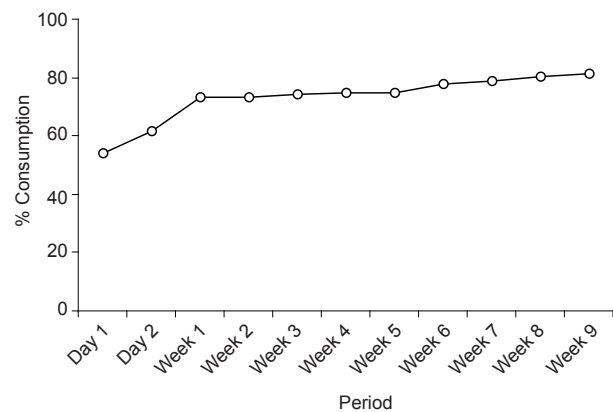

Figure 3. Pattern of food consumption by *C. sphinx* (n = 15) over nine weeks of captivity.

Table 1. Nutritional value of average fruits consumed by *C. sphinx* in captivity

Fruit consumption		Unit	Banana	Apple	Pears	Guava	Papaya	Total fruit
15 bats / week								
Weight		g	3834.69	2801.29	780.25	586.09	1360.92	9363.25
1 bat / day								
Weight		g	36.52	26.68	7.43	5.58	12.96	89.17
Water		%	74.6	83.6	84.0	86.7	88.6	
Energy	[1]	Kcal	26.30	13.61	3.27	3.85	4.15	51.17
	[2]	Kcal	33.60	15.74	4.38	2.85	5.05	61.63
	[3]	Kcal	39.81	15.47	3.20	2.29	3.50	64.26
Protein		g	0.32	0.00	0.04	0.06	0.09	0.51
Carbohydrates	[1]	g	6.57	3.52	0.85	0.97	1.09	13.00
	[2]	g	8.65	4.12	1.11	0.68	1.30	15.87
	[3]	g	10.55	3.74	0.74	0.64	0.80	16.48
Fibers		g	0.61	0.58	0.19	0.33	0.12	1.84
Fat		g	0.38	0.02	0.04	0.07	0.01	0.53
Saccharides		g	0.03	0.02	0.01	0.02	0.01	0.10
Ca	[1]	mg	3.65	2.67	0.74	0.84	2.20	10.10
	[2]	mg	2.24	1.94	0.82	1.12	3.15	9.26
	[3]	mg	2.19	4.00	0.30	1.12	2.20	9.81
P	[1]	mg	8.77	2.67	1.11	1.34	2.07	15.96
	[2]	mg	7.05	1.94	0.82	1.43	0.65	11.88
	[3]	mg	6.57	1.60	1.04	1.56	1.56	12.33
Na		mg	0.32	0.00	0.04	0.19	0.37	0.91
K		mg	144.48	30.56	9.29	15.88	33.24	233.44
Zn		mg	0.06	0.00	0.01	0.01	0.01	0.09
Fe		mg	0.13	0.05	0.02	0.02	0.01	0.22
Mg		mg	10.57	1.21	0.45	0.56	1.30	14.08
Vit A		RE	2.88	1.46	0.15	4.40	26.11	35.00
Vit C		mg	3.20	1.46	0.30	10.23	8.05	23.24
Vit B6		mg	0.21	0.01	0.00	0.01	0.00	0.24
Folate		micg	7.05	0.73	0.56	0.81	4.91	14.05
Amino acids		mg	0.24	0.03	0.01	0.07	0.05	0.42

[1] - FAO (1995); [2] - or without notation - Smolin & Grosvenor (1994); [3] - Center for Food Safety Hong Kong (1997)

77% and reached up to 81% in the following weeks. We also found significant increase in food consumption per bat in relation to time between the two captive conditions (least square regression analysis: $p < 0.01$; and $p < 0.001$, respectively). Papaya (53%) made the maximum portion of the left fruit.

Consumption of apple and banana ranked at par with 89% and 93%, respectively. The consumption of fruits decreased significantly in the small cage ($\chi^2 = 32.8$, df = 1, $p < 0.05$ and confirmed performing two-tailed Wilcoxon signed-ranks test, $t = 0$, $n = 8$, $p < 0.02$). Compared to the flight cage where the consumption ranged from 70–80 % of the offered fruit, the same got reduced to 30–45 % in the small cage. There was significant difference in fruit consumption when compared between flight cage and in the small cage (two way ANOVA, $F = 5.43$, df = 2, $p < 0.01$). The papaya made the bulk (75%) of left out fruit. Unlike in the flight cage, where the consumption percentage increased over the period of captivity, in the small cage the consumption percentage showed a decreasing trend over a period of four weeks (45.6, 41.9, 44.8, 38.1 & 30.3 %, respectively) (Fig. 3). Daily dietary intake and nutritional values. The average daily consumption of fruit per 15 bats was 400.18g apple, 547.81g banana, 83.72g guava, 194.42g pear, and 111.46g papaya. Thus, the daily food consumption of food per bat was 36.52g banana, 26.68g apple, 7.43g pear, 5.58g guava, and 12.96g papaya in the flight cage. The conversion and deduction of the total weekly fruit consumption of 15 bats to an individual bat per day equates to 269.03kJ of energy that is required while in captivity based on the nutritional values obtained from Centre for Food Safety Hong Kong (2006), the same consumption deduced to only 214.27kJ based on FAO 1995 values.

The water content of papaya (0.88g g^{-1}) is higher than for all the other fruits. Banana provides twice the amount of carbohydrate (0.24g g^{-1}) as compared to papaya (0.1 g g^{-1}). The comparison of fruits displaced in terms of energy gain, showed that banana and papaya provide the highest (0.72–1.09 Kcal g^{-1}) and the least (0.39–0.27 Kcal g^{-1}) amount of energy, respectively note that the lower and higher values were from FAO (1995) and Centre for Food Safety Hong Kong (2006), respectively.

To assimilate 69.03kJ, a bat needs to consume 200–238 g of papaya but only 59–89 g of banana. Conversely, 200g of papaya means that an average male bat would be required to consume more than four times its body weight per night. The amount of fruit consumed and the respective nutritional contents are given in Table 1.

Comparisons of body mass changes

The initial average body mass on catch was 48.4g and 53.0g for male and female, respectively. The average body mass decreased within the first two weeks after catch but later regained the weight of the original body mass. The female bats showed comparatively higher gain

in body mass than the males (sign test; $x = 1$, $n = 10$, $p < 0.03$). The overall body mass did not differ significantly over the captive period of nine weeks (Fig. 4a). The average body mass of bats in the small cage showed a declining trend but was not significant (ANOVA {time/body mass}): $p > 0.05$ over the four-week experiment (Fig 4b). With an average reduction from 55g to 46g and from 50g to 46g the females lost more weight than the males, respectively.

DISCUSSION

Cynopterus sphinx generally ate all fruits that were offered. However, large differences existed in the consumption relative to fruit species. Banana was the most preferred fruit followed by apple. Neither guava nor pear was consumed in the same amounts, and papaya was the least preferred of the fruits. While banana, papaya and guava are abundantly available throughout the area, both apple and pear represent introduced fruit. With caloric values of 0.27, 0.41, 0.43, 0.58 and 1.09 Kcal g^{-1}, the five fruits papaya, guava, pear, apple and banana lined up along a positive trend of consumption increasing with the caloric value based on the nutritional values obtained from the Centre for Food Safety Hong Kong (2006). Even with deviating values for apple and pear, the nutritional contents published by Smolin & Grosvenor (1994) corroborate the overall trend. FAO (1995) presented significantly lower (0.72 Kcal g^{-1}) and higher (0.69 Kcal g^{-1}) caloric values for Chinese banana and guava, respectively, which was reflected by giving a broader range of minimum energy requirement.

Still, a single fruit-related character such as energy content, abundance of resources or its exoticness may not fully explain the food preference of the bats. Few reports on food preference in bats include similar fruit. However, lowest preference for papaya was also reported for flying foxes (Banack 1998), which fed on papaya mainly during periods when alternative fruits where not available or not ripe. Contradictorily, the *C. sphinx* consumed/ preferred papaya over other fruits and banana was the least preferred fruits (Elangovan & Marimuthu 2001).

The daily energy expenditure of the bats in captivity can be divided between the long roosting phase and a shorter activity phase when they fly around the food resources. It seems important to estimate the amount of energy bats need while in confinement. From the present study it appears that the daily intake of food varied according to their demand of energy expenditure for movement and during resting. The total consumption of fruit was significantly lower (roughly 30–40 %) for animals in flight-restrictive cages, reflecting less activity and hence lower energy requirements. Banack (1996, 1998) reported bats in the wild being extremely selective in choosing fruit within a tree, smelling and occasionally biting 10–15
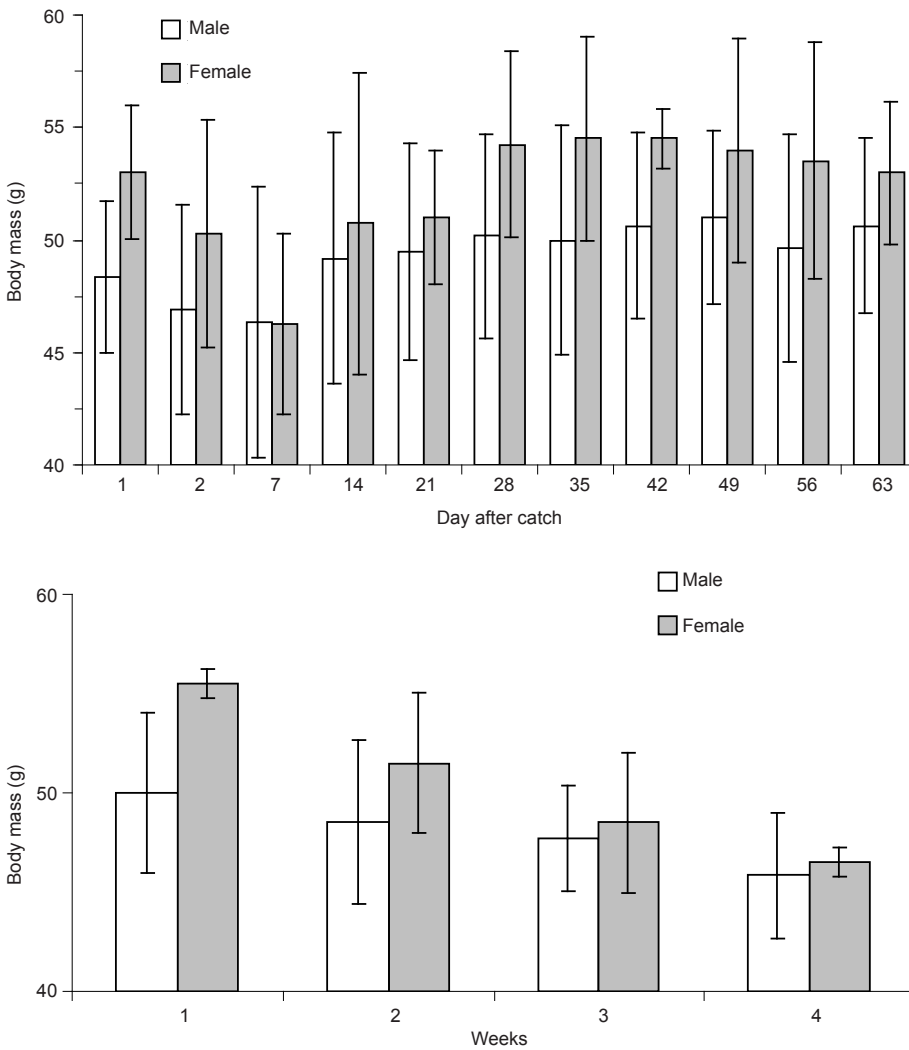
Figure 4a, b. Change in average body mass of *C. sphinx*: a). (n = 15) over a period of 63 days in a flight cage, b). (n = 6) over a period of four weeks in a small cage.

fruits before choosing one in situ or flying to another tree to continue the search. Such hyper-selective searching requires much higher energy input and may probably be less frequent under conditions of food scarcity.

In the flight cage, where the bats had to fly to get food, the individual bat consumed on average an energy equivalent to about 269kJ (FAO 214.27kJ) per day. The validity of this value may underly some restrictions, because factors such as the environment and variations in both (seasonal) climate, handling-time efficiencies and physiological or morphological state can alter requirements in nutrients and secondary compounds (Rosenzweig & Sterner 1970; Willson & Harmeson 1973; Ellis et al. 1976; Pierson et al. 1996). The daily energy expenditure by blossom-bats in the laboratory is relatively high in winter, because they have long activity periods at night and undergo only short and shallow periods of torpor during the day (Coburn & Geiser 1996, 1998). According to (Voigt 2000b, 2004; Voigt & Winter 1999) the power requirements of horizontal forward flight are known to

increase with body mass and thus mass-dependent costs of locomotion could substantially contribute to the overall higher energy expenditure of large individuals. Again, it is important to mention that the main phase of experiments was conducted during the month with lower temperatures, and hence in order to maintain homeostasis the bats may have used a higher proportion of energy even during resting. Furthermore, the daily energy intake averaged over both male and female and different ages, but did not reflect increased requirements due to pregnancy or lactation of female bats, which breed in area throughout the year (Mukherjee et al. 2006).

Despite differences in diet and feeding strategy among mammals, most species that have been studied appear to have similar qualitative nutrient needs for normal tissue metabolism. These similarities may also be true for fruit bats. Fruit bats presumably have no difficulty meeting energy needs during periods of food abundance because they consume large amounts of high carbohydrate fruits, both in captivity and in the wild. Analyses of most

cultivated fruits indicate that the concentrations of many nutrients are quite low. Compared to established nutrient requirements of other mammals and the foods needed to provide them, fruit, when consumed alone, would seem to constitute an inadequate diet regarding their low protein content. However, several studies concluded that fruit bats could meet their protein requirements exclusively with fruits (Thomas 1984; Herbst 1986; Stellar 1986; Conklin-Brittain et al. 1999; Delorme & Thomas 1999).

Occasional observations also revealed that some bats feed on leaves of some ficus species (A. Mukherjee pers. obs.; Korine et al. 1999; Nelson 2000). Pierson et al. (1996) reported that leaf resources may represent a regular part of the diet following major disturbances and during the breeding season.

Bats are one of the only other mammals besides humans that have problems with calcium deficiency, and reproduction by female bats may be limited by their intake of calcium. Nelson (2000) found that 83% of the captive bats engaged in leaf eating, and that 70% of female bats ate leaves, a particularly important calcium source. Bats may prefer high sugar containing and succulent fruits to relieve hypoglycaemia and dehydration. At least during the low-temperature months of our experiments the bats showed no particular preference for a special calcium-rich or a special Ca/P-ratio containing diet. However, such particular preferences may develop during other seasons and particularly during pregnancy. Furthermore, the way fruit bats eat, i.e., ingesting mostly juices and rejecting the fibrous portion of fruits, may result in higher bio-availability of the consumed calcium.

C. sphinx in our flight cage experiment behaved similar to wild-caught Short-tailed Fruit Bats (*Carollia perspicillata*), which reportedly rested for approximately 30min between foraging bouts when the bats were kept in an outdoor enclosure (Bonaccorso & Gush 1987). Short-tailed Fruit Bats have an extremely sensitive sense of smell (Laska 1990a) and are proficient at discriminating between similar odours (Laska 1990b) and olfaction is more important than either vision (Laska & Schmidt 1986; Mikich et al. 2003) or echolocation (Theis et al. 1998) for the detection and gross location of food. *C. sphinx* appears to follow the same cue to locate food resources (Mukherjee et al. 2006). Again similar to the Short-tailed Fruit Bat, which showed the most diverse diet among several frugivorous bat species in Costa Rica (Fleming et al. 1977; Fleming 1988), *C. sphinx* showed preferences but otherwise consumed all the offered species of fruit. Based on our occasional observation over a period of three years while working in the rain forest, our study also suggests that *C. sphinx* is a dietary generalist (Table 2). Therefore, we have to assume that it must either use familiar food resources, which may be of low quality or ephemeral, or sample unknown and possibly toxic foods (Day et al. 2003; Ratcliffe et al. 2003) and might be operating on an overall tight energy budget (Delorme &

Table 2. The plant exploited by *C. sphinx* in Xishuangbanna Tropical Botanical Garden

Family	Species	Plant part
Anacardiaceae	*Mangifera indica*	Fruit
Euphorbiaceae	*Sapium baccatum*	Fruit
Moraceae	*Ficus hispida*	Fruit
	Ficus racemosa	Fruit
	Ficus hederacea	Fruit
	Ficus benjamina	Fruit
	Ficus religiosa	Fruit + leaf
	Morus macroura	Fruit
	Ficus callosa	Fruit
	Ficus ischnopoda Miq.	Fruit
	Ficus tinctoria	Fruit
	Ficus fistulosa	Fruit + leaf
	ficus annulata	Fruit
Myrtaceae	*Psidium guajava*	Fruit
	Syzygium oblatum (Roxb.) Cowan (Wall.)	Fruit
	Syzygium fluviatile (Hemsl.) Merr. et Perry	Fruit
Rosaceae	*Pygeum latifolium*	Fruit
Sapindaceae	*Nephelium lappaceum*	Fruit
	Litchi chinwnsis	Fruit
	Dimocarpus lognan	Fruit
	Sapindus rarak	Leaf
Sapotaceae	*Achras sapota*	Fruit
Musaceae	*Musa acuminata*	Fruit + nectar
Rubiaceae	*Anthocephalus chinensis*	Fruit
Rhizophoraceae	*Pellacalyx yunnanensis*	Fruit
Ebenaceae	*Diospyros nigrocartex*	Fruit
Lauraceae	*Beilschmiedia purpurascens*	Leaf
Flacourtiaceae	*Flacourtia ramontchii* L. Herit	Fruit
Solanaceae	*Solanum verbacifolium* Linn.	Fruit

Thomas 1996).

Specific nutrient requirements for frugivorous bats remain virtually unknown, however, information exists providing practical guidelines to formulate diets for certain bat species in captivity. Research opportunities in bat nutrition proliferate, and regarding the bat species diversity, the information derived from a detailed diet plan for a large species would improve not only dietary husbandry of this species, but our understanding of the potential nutrient requirements of other species with similar dietary habits and feeding strategies.

Our study provides important information on food preferences and energy requirements for *C. sphinx* in captivity, and it may contribute to succesful captive breeding and conservation of the species. To improve diet

formulas for fruit bats in long-term captivity, future research may put more focus on identifying the food combinations appropriate for meeting needs in micro-nutrients. It seems obvious that energy requirements for resting and for flight in captivity can be met by offering ad libitum quantities of nutritionally appropriate food, especially because fruit eating bats readily accept cultivated fruits. However, more detailed understanding of diets from bats in captivity also contributes to our understanding of bats in the wild.

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