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Food transit times and carbohydrate use in three Phyllostomid bat species

By M. LASKA

Zoological Institute of the University of Bonn, F.R.G.

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Abstract

Studied were the food transit times and carbohydrate use in three species of frugivorous microchiroptera. Food passed through the digestive tract very quickly, averaging from 22.3 ± 4.2 minutes in *Carollia perspicillata* to 33.6 ± 3.4 minutes in *Phyllostomus discolor* (mean \pm S.D.; N = 12 trials respectively). The mean value of "additional load", i.e. the amount of food consumed before starting to defecate, was 3.95 ± 0.4 g of banana in *Carollia* (mean \pm S.D.; N = 40 trials), corresponding to 22 % of body weight.

The highest uptake of the soluble carbohydrates sucrose, glucose and fructose was found in *Sturnira lilium* (92.9 %), the poorest in *Phyllostomus* (86.6 %). Lactating female *Carollia* displayed a higher degree of sugar uptake (91.5 %) than conspecifics (89.2 %) while food transit times were unchanged.

A suboptimal but still satisfactory use of carbohydrates in combination with remarkably short food transit times seems to be the best strategy to maximize energy gain in frugivorous Phyllostomids eating a low-quality diet.

Introduction

Homoeothermy and locomotion by active flight are properties that imply a high metabolic rate. While many studies have investigated the composition and variety of diet in bats (WILSON 1973; GARDNER 1977) there is only sparse information about the uptake of food by the digestive system (KEEGAN 1975).

Active fliers should have to minimize their mass intake of food but at the same time maximize their energy intake. Optimal foraging is one important factor helping to solve this dilemma (FLEMING and HEITHAUS 1986; FLEMING et al. 1977). Concerning a second factor, i.e. the digestive abilities of a bat, two different strategies are possible to maximize the energy yield from food: 1) Either small quantities of food are consumed at a time and totally processed or 2) large amounts are passed through the intestine quickly with suboptimal uptake.

These two strategies are not exclusive, but mark extremes on a continuum of possible behaviors, which are influenced by the abundance of high- or low-quality food.

I became aware of this problem through the observation that frugivorous bats already begin defecating a few minutes after the start of a food-rewarded flight training. The purpose of this study was to systematically investigate food transit times through the alimentary canal and determine energy uptake in order to clarify, which of the above mentioned strategies are used by frugivorous bats on a given diet.

Material and methods

Animals of the three phyllostomid bat species *Carollia perspicillata* (3 ♂; 3 ♀), *Phyllostomus discolor* (3 ♂; 3 ♀) and *Sturnira lilium* (2 ♀) were taken from captive colonies maintained at the Zoological Institute of Bonn University.

I measured the food transit times of animals which were transferred daily into solitary cages. At

the same time of day (one hour after the dark cycle began) **mashed ripe banana was offered as food** ad libidum. Every other day this mash was stained with a **commercial food dye** ("chocolate brown" by Fa. Brauns-Heitmann, Warburg) to indicate the transit of freshly consumed food.

I observed the animals' feeding behavior and determined food transit times using an infra-red nightvision scope.

The maximal "additional load", i.e. the quantity of food a bat swallowed before starting to defecate, was determined in 4 male *Carollia*. These animals were exclusively fed during a flight-training and rewarded with pieces of banana (150 ± 10 mg) in every test trial which allowed exact correlation of consumed quantities and times of intestinal passage.

The percentage of the carbohydrates sucrose, glucose and fructose in the banana and in the feces of the animals was analysed by UV-spectral photometry. For this the samples were dehydrated, ground, dissolved in aqua dest. and the following enzymatic preparation (BOEHRINGER 1973) applied:

1. Sucrose + $H_2O \rightarrow \beta$ -Fructosidase \rightarrow Glucose + Fructose
2. Glucose + ATP \rightarrow HK \rightarrow G-6-P + ADP
3. Fructose + ATP \rightarrow HK \rightarrow F-6-P + ADP
4. G-6-P + $NADP^+ \rightarrow$ G-6-P-DH \rightarrow Gluconat-6-P + NADPH + H^+
5. F-6-P \rightarrow PGI \rightarrow G-6-P

The amount of NADPH is proportional to the amount of glucose and was measured at 340 nm. The degree of sugar uptake is expressed in terms of the percentage ratio between the sugar contents of food and feces. This is a valid approximation of the real sugar uptake as the dry weight composition of food and feces in this case is nearly identical.

In order to investigate a possible influence of lactation or temporal reduction of food access on food transit times and digestion, two additional experimental groups of *Carollia* were examined: Group "L" consisted of two lactating females (8 to 14 days post-partem), group "F" of two males being accustomed to a shortened food access of only three hours per day.

I report all the data as means \pm S.D.

Results

The food transit times of the three species investigated are significantly different (ANOVA $F = 31.674$; $p < 0.001$; LSD-test: C./S.: $p < 0.05$; S./P.: $p < 0.01$) (Table 1).

Compared to insectivorous species (BUCHLER 1975; LUCKENS et al. 1971) the retention time of food in the digestive tract of frugivorous bats are lower. Within the frugivores there seems to be a positive correlation between food transit time and body mass.

In contrast to the findings in *Myotis lucifugus* (BUCHLER 1975), no connection between the value of transit time and the level of activity in *Carollia* was found. Animals exclusively feeding during a flight training did not exhibit statistically different values for intestinal passage compared to caged conspecifics (24.4 ± 4.5 minutes; $N = 40$ trials / 22.3 ± 4.2 minutes; $N = 12$ trials; $t = 1.438$; $p > 0.10$).

There were no sex-dependent differences in food transit times for either *Carollia* ($\delta = 23.3 \pm 4.3$ min; $\eta = 21.3 \pm 4.2$ min; $N = 6$ per group; $t = 0.815$; $p > 0.20$)

Table 1. Food transit times in three Phyllostomid bat species compared to data by other authors

	transit time (min)	body weight (g)	feeding habit
<i>Carollia perspicillata</i>	22.3 ± 4.2	18	F
<i>Sturnira lilium</i>	25.7 ± 3.0	20	F
<i>Phyllostomus discolor</i>	33.6 ± 3.4	35	O
<i>Rousettus aegyptiacus</i>	46	130	F (KEEGAN 1977)
<i>Artibeus jamaicensis</i>	30	50	F (MORRISON 1980)
<i>Eptesicus fuscus</i>	122	20	I (LUCKENS 1971)
<i>Myotis lucifugus</i>	46-144	8	I (BUCHLER 1975)
Results are shown in terms of mean \pm S.D. $N = 12$ trials per group ; F = Frugivorous; I = Insectivorous; O = Omnivorous			

or *Phyllostomus* ($\delta = 33.7 \pm 2.9$ min; $\varphi = 33.5 \pm 4.2$ min; $N = 6$ per group; $t = 0.096$; $p > 0.20$).

I also found no evidence for variation in food transit time with reproductive conditions or under conditions of food limitation. Lactating females (group "L") of *Carollia* show no statistically significant longer passage times than non-lactating conspecifics (23.7 ± 4.6 minutes; $N = 6$ trials / 21.3 ± 4.2 minutes; $N = 6$ trials; $t = 0.944$; $p > 0.20$). The contrary is reported for the insectivorous *Myotis lucifugus* (BUCHLER 1975).

The experimental group "F" of male *Carollia*s likewise showed no significant differences in transit times compared to normal males having food access during the whole dark cycle (22.4 ± 4.2 minutes; $N = 6$ trials / 21.3 ± 4.2 minutes; $N = 6$ trials; $t = 0.454$; $p > 0.20$).

Carollia starts to defecate after having consumed an amount of 3.95 ± 0.4 g banana on the average ($N = 40$ trials) (Fig. 1). This corresponds to an "additional load" of 22 % of body mass. The maximum value found was 4.8 g, equivalent to 27 % of body mass. As *Carollia* is able to fly even with a load of about 50 % – this is the case while carrying a three-week-old pup – the observed momentary maximum of nutritive load seems to be due to a complete filling of the alimentary canal.

No significant interindividual differences were found in this respect. However, there is a significant relation ($y = 8.5x - 9.06$; $r = 0.77$) between the mass of food ingested and transit time. Food staining indicated that all three species empty their digestive tracts completely prior to the next day's meal, unlike the insectivorous *Eptesicus fuscus*, whose first fecal pellets consist of the final remains of the previous day's food (LUCKENS et al. 1971). The quantitative ratio of the three saccharids in the banana correspond (Table 2) well with data found by other authors (FORSYTH 1980). The same is true for the water content in the ripe fruit.

The three bat species differ significantly in the degree of sugar uptake (ANOVA $F = 18.86$; $p < 0.001$; LSD-test: C./S.: $p < 0.01$; C./P.: $p < 0.05$).

The soluble carbohydrates are best exploited by *Sturnira* (92.9 %) while *Phyllostomus* displays the poorest degree of sugar uptake (86.6 %). Considering the very short transit times the data suggest a highly efficient carbohydrate resorption in the intestine.

With *Carollia*, showing an average sugar uptake of 89.2 %, the experimental group "F" proved to be unimpaired (89.0 %) in its digestive abilities. Lactating females of *Carollia* (group "L") seem to score better (91.5 %) than their conspecifics. This fact is probably due to milk production, just like the distinctly decreased water content of their feces.

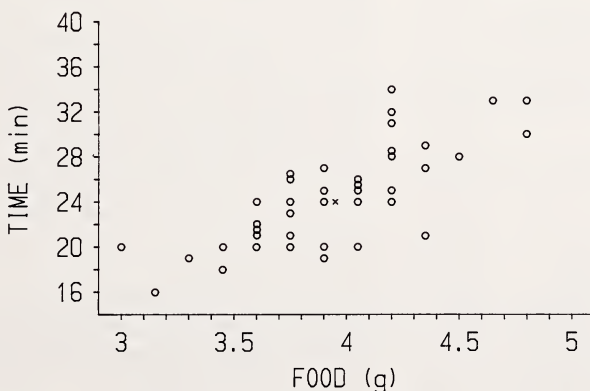


Fig. 1. Distribution of food transit times as a function of the amount of food consumed before starting to defecate in *Carollia perspicillata*. × indicates the mean value of the "additional load"

Table 2. Percentage of soluble carbohydrates and water content in food and feces of Phyllostomid bats

	sucrose	glucose	fructose	sugar total	sugar uptake (%)	water content
Banana	19.9 ± 1.2	7.9 ± 2.3	8.8 ± 1.7	36.6 ± 5.1		74.5 ± 1.3
<i>Carollia perspicillata</i>	0.65 ± 0.09	1.07 ± 0.10	2.23 ± 0.18	3.96 ± 0.22	89.2	79.8 ± 1.3
<i>Phyllostomus discolor</i>	1.33 ± 0.41	1.78 ± 0.48	1.81 ± 0.38	4.91 ± 0.82	86.6	79.9 ± 2.0
<i>Sturnira lilium</i>	0.57 ± 0.07	1.56 ± 0.15	0.46 ± 0.29	2.60 ± 0.37	92.9	76.4 ± 2.4
<i>Carollia</i> "F"	0.77 ± 0.15	1.23 ± 0.20	2.04 ± 0.33	4.04 ± 0.31	89.0	79.1 ± 1.9
<i>Carollia</i> "L"	0.44 ± 0.18	0.91 ± 0.09	1.75 ± 0.28	3.10 ± 0.36	91.5	76.3 ± 2.0

Results are shown in terms of mean ± S.D.; N = 4 trials per group. Sugar values in % dry weight; water content in % fresh weight. Sugar uptake in terms of percentage ratio between sugar contents of food and feces.

In each of the five experimental groups a urine sample was analysed. None of them contained soluble carbohydrates.

Discussion

Neotropical bats feed on a variety of fruits and parts of plants but prefer certain species. This could be due to a preference for high- or low-abundant fruits (BONACCORSO and GUSH 1982). *Carollia* may specialize on less-abundant *Piper* and *Muntingia* fruits, but show a fast, efficient and intermittent feeding behavior (BONACCORSO and GUSH 1981). *Artibeus jamaicensis* prefers super-abundant *Ficus* fruits and is a slow constant feeder, which achieves a high degree of energetic economy by efficiently sucking fruits dry instead of swallowing them (MORRISON 1980). This unusual mode of obtaining calories is also reported for some Megachiroptera (WOLTON et al. 1982).

Apart from the abundance of fruits their nutritive value can control the bats' feeding behavior (THOMAS 1984). Tropical fruits generally have a high percentage of carbohydrates, but often lack proteins and lipids (MORTON 1973). In this respect banana is representative for the food supply of tropical frugivores, showing a dry weight percentage of up to 70 % soluble carbohydrates but only 1.2 % proteins and 0.2 % lipids.

The soluble sugars sucrose, glucose and fructose make up more than 95 % of the digestible energy in ripe banana fruits (MARRIOTT and LANCASTER 1983).

The strikingly short food transit times found in this investigation at first suggest that bats use the second strategy of low efficiency high bulk food processing. The fact that the length of the intestine of frugivorous microchiroptera is only 1/3 to 1/2 of that of a rodent of comparable body weight (KLITE 1965) adds to this idea. The high values of carbohydrate uptake however, suggest that this extreme strategy is not applied. It appears to be advantageous for frugivorous bats to do without a complete (i.e. 100 %) sugar exploitation, but to keep it on a sufficiently high level in order to avoid the need for large quantities of food.

The daily energy budget of a bat can be estimated by measurements of oxygen consumption (McNAB 1969) and results in the following for the species of this investigation:

<i>Carollia perspicillata</i>	5.2 (+ 1.3) Kcal/d
<i>Sturnira lilium</i>	6.4 (+ 1.6) Kcal/d
<i>Phyllostomus discolor</i>	5.8 (+ 1.5) Kcal/d

The values in parentheses give the additional amount of energy needed for a net flying time of 30 minutes per night. They are based on the assumption that flight metabolism is approximately the 12-fold of the basal metabolic rate (THOMAS et al. 1984). As ripe banana fruit contains 96 Kcal/100 g of edible material, a daily minimum requirement of 6.8 g (*Carollia*), 8.3 g (*Sturnira*) and 7.6 g banana (*Phyllostomus*) can be calculated for freely flying animals. 5.4 g of banana, which is equivalent to the basal rate of metabolism in *Carollia*, corresponds well with the finding that caged animals of this species need about 5 g of this fruit per day to maintain their body weight when supplied with protein once a week (LASKA and SCHMIDT 1986).

I conclude that a suboptimal but still satisfactory use of carbohydrates in combination with strikingly short food transit times seems to be the best strategy to economize with energy in frugivorous Phyllostomids feeding on a low-quality diet.

The possible effects of a change of diet still have to be investigated.

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Zusammenfassung

Dauer der Nahrungspassage und Kohlenhydratverwertung bei Carollia perspicillata, Phyllostomus discolor und Sturnira lilium (Phyllostomatidae, Chiroptera)

Bei drei fruchtfressenden Fledermausarten der Neotropen wurden die Verweilzeiten der Nahrung im Verdauungstrakt und die dabei erzielte Kohlenhydratausbeute untersucht. Anhand gefärbten Futters wurden sehr kurze Darmpassagezeiten nachgewiesen, die von 22.3 ± 4.2 Minuten bei *Carollia perspicillata* bis zu 33.6 ± 3.4 Minuten bei *Phyllostomus discolor* reichten ($x \pm s$; jeweils $N = 12$).

Die maximale Futtermenge, die vor Einsetzen der Defäkation aufgenommen wurde, betrug bei *Carollia* im Mittel 3.95 ± 0.4 g Banane. Dies entspricht 22 % des Körpergewichtes.

Die höchste Resorptionsrate der Kohlenhydrate Saccharose, Glucose und Fructose erzielte *Sturnira lilium* mit 92,9 %, die niedrigste *Phyllostomus discolor* mit 86,6 %. Laktierende *Carollia* zeigten eine höhere Zuckeraufnahme (91,5 %) als ihre Artgenossen (89,2 %), wobei die Transitzeiten der Nahrung unverändert blieben.

Eine suboptimale, aber hinreichend hohe Ausnutzung der Kohlenhydrate scheint im Zusammenspiel mit sehr kurzen Verweilzeiten der Nahrung im Körper die ökonomischste Strategie zur Energiegewinnung bei frugivoren Phyllostomatiden zu sein.

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Author's address: Dr. MATTHIAS LASKA, Zoological Institute, University of Bonn, Poppelsdorfer Schloß, D-5300 Bonn 1, F.R.G.