RESEARCH ARTICLE

Digestive efficiency of Knysna and purple-crested turacos fed varying concentrations of equicaloric and equimolar artificial fruit

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SUMMARY

Avian frugivores have been somewhat poorly studied with regards to the effects that different fruit sugar types and concentrations have on their digestive efficiencies. Therefore, two relatively large South African frugivores, the Knysna turaco (*Tauraco corythaix*) and the purple-crested turaco (*Gallirex porphyreolophus*), were fed artificial fruit that contained equicaloric and equimolar concentrations of different sugars, to determine their daily food and energy intake, digestive efficiencies and digestive transit times. The artificial fruit contained 6.6, 12.4 or 22%, or 0.42, 0.83 or 1.66 mol l^{-1} sucrose or glucose. Food intake of both turaco species increased with decreasing sugar concentration and molarity, irrespective of sugar type, suggesting compensatory mechanisms for energy requirements. Apparent assimilation efficiencies of both turaco species ranged from 61.4–90.0% and 60.2–92.4% for equicaloric and equimolar artificial fruit diets, respectively. Digestive transit times for both turaco species were slowed with an increase in sugar concentration and molarity, irrespective of sugar type. Consequently these two frugivores appear to be tolerant of sugar type and would be expected to select fruits based on energy yields. Future studies of the composition of indigenous forest fruit sugars may give insight into food preferences of the turaco species and their role as potential seed dispersers of fruiting tree species.

Key words: sugar type, sugar digestion, frugivory, Knysna turaco, purple-crested turaco, artificial fruit, forest fruit.

INTRODUCTION

The amount of energy available in the different food types will influence the amount of food consumed by the individual (Ayala-Berdon et al., 2008) with intake levels usually being reduced as levels of available energy increase (Slansky and Wheeler, 1992). This 'intake response' (Castle and Wunder, 1995) has been well studied in nectarivorous birds (Collins, 1981; López-Calleja et al., 1997; McWhorter and Martínez del Rio, 2000), but remains poorly understood in frugivorous birds (see Levey and Martínez del Rio, 1999). This inverse relationship between nutritional levels and food intake has often been attributed to compensatory feeding (Simpson et al., 1989) where the amount of food eaten is regulated to maintain a constant amount of assimilated energy (Montgomery and Baumgardt, 1965; Slansky and Wheeler, 1992).

Many studies have examined the effects of sugar type and concentration on food preferences, digesta transit times, digestive efficiencies and food intake in nectarivorous birds (Tamm and Gass, 1986; Downs and Perrin, 1996; Downs, 2000; Schondube and Martínez del Rio, 2003; Brown et al., 2008; Fleming et al., 2008; Brown et al., 2010). Digesta transit times are important as they may give an indication of how well nutrients are absorbed by the gut (Witmer, 1998a). Avian frugivores, in contrast to avian nectarivores, have been poorly studied with regards to the effects that different fruit sugar types, concentrations and molarities have on their digestive efficiency (Levey and Martínez del Rio, 1999; Levey and Martínez del Rio, 2001; Lotz and Schondube, 2006). Although fruit choice by avian frugivores may be influenced by a number of non-nutritive factors such as fruit colour, size and secondary compounds (Murphy, 1994), the bird's digestive ability and the fruit's nutritional value are

considered to be important factors (Martínez del Rio and Restrepo, 1993; Johnson et al., 1985; Izhaki, 1992; Fuentes, 1994). Indeed, Worthington suggested that digestion is likely to be the most important restriction placed on avian frugivores (Worthington, 1989).

Fleshy fruits are roughly regarded as being either nutrient dense or nutrient dilute (Izhaki, 1993). Nutrient-dense fruits are considered to be relatively high in lipids, low in water and carbohydrates and variable in protein (Izhaki, 1993) whereas nutrient-dilute fruits are high in water, have fewer carbohydrates than lipid-rich fruits and are low in fibre and protein (Snow, 1981; Herrera, 1982; Izhaki, 1993). Most fruits are nutrient dilute (Levey, 1987) therefore, avian frugivores need to consume large amounts or only select those fruits that are nutrient rich (Worthington, 1989).

Fruit choice by some avian frugivores may be affected by their ability to digest the different sugars efficiently (Avery et al., 1999). Several studies have shown that some families from the Sturnid–Muscicapid lineage are unable to digest sucrose efficiently (Schuler, 1983; Martínez del Rio, 1990; Martínez del Rio and Restrepo, 1993; Levey and Martínez del Rio, 2001). This is explained by a lack of the enzyme sucrase in these species, without which sucrose cannot be hydrolysed into glucose and fructose, which can be easily assimilated (Martínez del Rio et al., 1988; Martínez del Rio et al., 1989; Martínez del Rio and Stevens, 1989; Karasov and Levey, 1990; Malcarney et al., 1994). Even those birds that do possess sucrase may prefer hexose sugars in choice tests because they may not be able to digest sucrose efficiently enough (Martínez del Rio et al., 1992; Avery et al., 1995).

There is little information on the sugar content of fruits that are consumed by most non-passerine frugivorous birds (e.g. pigeons,

hornbills, trogons and turacos) (Snow, 1981; Levey and Martínez del Rio, 2001; Lotz and Schondube, 2006). These birds play an important role in plant reproduction, as seed dispersal agents (Herrera, 2002), and some orders such as the African turacos (Musophagiformes) consist exclusively of frugivores (Kissling et al., 2009). Therefore, the sugar preferences and the digestion of different sugar types at varying concentrations and molarities were investigated in two non-passerine, relatively large avian frugivores, the Knysna (*Tauraco corythaix* Wagler 1827) and purple-crested (*Gallirex porphyreolophus* Vigors 1831) turacos (Musophagiformes: Musophagidae).

The aim of the study was to determine if digestion efficiency was affected by sugar concentration and type. Equicaloric artificial fruit were first used and then the experiments were repeated using equimolar artificial fruits to show the possible importance of energy in foraging decisions. It was hypothesized that sugar type and concentration would affect digestion in the two species of turacos. It was predicted that both species would: (1) have slower digesta transit times as concentration and molarity increased; (2) reduce their intake times as sugar concentration increased, irrespective of sugar type, as suggested by Simpson et al.'s compensatory feeding hypothesis (Simpson et al., 1989); and (3) have high apparent assimilation efficiency, irrespective of sugar type, as shown by Martínez del Rio and others (Martínez del Rio, 1990; Lotz and Nicolson, 1996; Jackson et al., 1998; Witmer, 1999).

Knysna turacos are relatively large (*ca.* 310 g), fairly common, forest (Oatley, 1997) frugivores that are endemic (Rowan, 1983) to South Africa (du Plessis and Dean, 2005a). Similarly, purple-crested turacos are relatively large (*ca.* 300 g) locally common frugivores with part of their distribution in lowland forests in eastern South Africa (du Plessis and Dean, 2005b). Although both species are typically resident, they may locally track fruit in response to availability (Rowan, 1983).

Owing to a lack of knowledge of the sugars of South African fruits, we were unable to devise an artificial fruit diet that reflected typical ranges of the nutritional composition of indigenous, bird-dispersed fruits in South Africa. In this study, we therefore used the same artificial fruit glucose diet (Table 1) as Witmer and our artificial diet consequently has similar sugar and protein content to bird-dispersed sugary fruits in the United States (Witmer, 1998a). This artificial diet controlled for the effects of seeds and secondary compounds that are known to affect digestion (Bairlein, 1996; Cipollini and Levey, 1997; Fukui, 2003). A second artificial diet was used in which equicaloric sucrose replaced glucose, and a third artificial diet was used in which equimolar sucrose replaced glucose (Table 1).

Table 1. Composition of the three equicaloric and three equimolar artificial fruit diets used

Ingredients	Diet composition (g)		
	Low	Medium	High
D-glucose	75	150	300
Equicaloric sucrose	71.2	142.4	284.8
Equimolar sucrose	142.47	284.93	569.87
Water	1000	1000	1000
Wheat bran	50	50	50
Agar	10	10	10
Sodium chloride	0.75	0.75	0.75
Dicalcium phosphate	0.80	0.80	0.80
Vitamin supplement	0.75	0.75	0.75

MATERIALS AND METHODS
Bird capture and maintenance

Nine captive-bred Knysna turacos and four captive-bred purple-crested turacos were sourced from Mr M. C. Weber (Vryheid, KwaZulu-Natal, South Africa) under permit from Ezemvelo KZN Wildlife (permit number: 1781/2008). One purple-crested turaco was borrowed from Mr R. Poley (Durban, KwaZulu-Natal, South Africa). The birds were housed in pairs (with the exception of the loaned bird that was housed individually) in outside aviaries (1×2.12×2.66 m) for 1 week before experiments were conducted. A maintenance diet was fed daily. The maintenance diet consisted of a choice of mealworms (*Tenebrio molitor* larvae), pears, paw-paws, apples, carrots, bananas, oranges and/or grapes. The skin was removed from paw-paws, bananas and oranges and the flesh was cut into approximately 1×1×1 cm cubes. The other fruits were grated. A mixture of Aviplus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa) was added to the maintenance diets. Water was provided *ad libitum*.

Experiments

The birds were moved indoors for 1 week before any trials were conducted. During the experiments, birds were housed in individual cages (42.7×43×59.3 cm) in a constant environment room with a 12 h:12 h L:D photoperiod at 25±1°C. To ensure a post-absorptive state at the beginning of each experiment any uneaten food was removed at 18:00 h on the previous day, and no food was available overnight because birds did not feed at night.

The body mass (g) of the birds was measured daily, 30–40 min prior to the light phase (06:00 h) and again in the evening (18:00 h). All food items were measured to 0.01 g and body mass was measured to 0.5 g.

Digesta transit times and digestive efficiency of sucrose and glucose diet treatments were investigated using three equicaloric concentrations: low (6.6%), medium (12.4%) and high (22%); and then three equimolar concentrations: low (0.42 mol l⁻¹), medium (0.83 mol l⁻¹) and high (1.66 mol l⁻¹), following the methods of Witmer (Witmer, 1998a).

For each diet treatment, artificial fruits were made by mixing all the relevant ingredients into 1 litre of boiling water (Witmer, 1998a). Thereafter, the mixture was left to solidify, stirring all the while to ensure that the ingredients were dispersed evenly throughout the mixture. All dietary treatments were analysed for energy content (Animal Science, University of KwaZulu-Natal).

Digesta transit times and digestive efficiency of artificial fruit diets

On the experimental days, birds were provided with a weighed amount of food at 06:00 h. Each experimental diet was dyed with red food colouring (Moirs, Cape Town, Western Cape, South Africa). The time that the birds first ate and the first appearance of the dye in their excreta was recorded to determine digesta transit times. Each experiment was run for 12 h (from 06:00 h to 18:00 h). Controls of each experimental artificial diet were used to estimate evaporative moisture loss from uneaten food. Birds were fed the maintenance diet between experiments and not fed the artificial diet on any two consecutive days. Excreta and food samples were oven dried at 60°C to constant mass.

For each bird, overall daily food intake (DFI; measured as wet mass) was determined for the respective diet treatments. These were quantified by subtracting the mass of the food remaining from the amount given and accounting for desiccation. The DFI was converted to daily gross energy intake (GEI) by accounting

for the respective water content and multiplying by the energy content for the dry mass of each diet type. Daily excreta energy loss (EE) was calculated as the mass of dried excreta produced multiplied by its dry mass energy value. Daily energy assimilated (DEA) was calculated as GEI minus EE. Daily apparent energy assimilation efficiency (AE) was calculated as DEA divided by GEI, and was then squareroot transformed. Finally, for comparison, the data were converted to per gram individual body mass by dividing by the mean of the initial and final body mass on the day of experimentation. The above protocol was repeated for each diet treatment and each bird species.

Analyses

As the same birds were used repeatedly, digesta transit time, body mass, GEI, DEA and food intake rates were compared with a generalised linear model repeated measures of analysis of variance (GLM RM ANOVA) and *post hoc* Tukey's tests, using STATISTICA version 7 (Statsoft, Tulsa, OK, USA). All values are means ± s.e.m.

RESULTS

Equicaloric digesta transit times

For Knysna turacos there were no significant differences in digesta transit times of the sucrose and the glucose artificial diet treatments at each concentration ($F_{2,16}$=0.93, P=0.415). Digesta transit times were slower with increasing glucose and sucrose concentrations, with the greatest variability for the glucose 6.6% equicaloric artificial fruit diet (Table 2). The 6.6% glucose artificial fruit diet had the fastest transit time (31.0±2.8 min, N=9) and the sucrose 22% artificial fruit diet had the slowest transit time (44.4±1.8 min, N=9; Table 2).

Similarly, for purple-crested turacos, there were no significant differences in digesta transit times of the sucrose and the glucose artificial diet treatments at each concentration ($F_{2,8}$=2.93, P=0.108). In addition, digesta transit times were slower with increasing glucose and sucrose concentrations, and unlike Knysna turacos they showed the greatest variability for the sucrose 12.4% artificial fruit diet (Table 2). In contrast to Knysna turacos, the sucrose 6.6% artificial fruit diet had the fastest transit time (20.6±1.6 min, N=5). Similar to Knysna turacos, the sucrose 22% artificial fruit diet had the slowest transit time (41.1±2.3 min, N=5; Table 2).

Equimolar digesta transit times

For Knysna turacos there were no significant differences in digesta transit times between the sucrose and the glucose artificial diet treatments at each concentration ($F_{2,16}$=0.88, P=0.435). Again digesta transit times were slower with an increasing glucose and sucrose molarity but with the greatest variability for the sucrose 1.66 mol l^{-1} artificial fruit diet (Table 2). The glucose 0.42 mol l^{-1} artificial fruit diet had the fastest transit time (31.0±8.4 min, N=9) and the sucrose 0.83 mol l^{-1} artificial fruit diet had the slowest transit time (65.5±5.2 min, N=9; Table 2).

Similarly, for the purple-crested turacos, there were no significant differences in digestive transit times between the sucrose and the glucose artificial diet treatments at each concentration ($F_{2,8}$=0.54, P=0.322). Digesta transit times were slower with increasing glucose and sucrose molarity with the greatest variability for the sucrose 0.42 mol l^{-1} artificial fruit diet (Table 2). The glucose 0.42 mol l^{-1} artificial fruit diet had the fastest transit time (24.6±1.3 min, N=5) and the sucrose 1.66 mol l^{-1}

Table 2. Body mass, transit time, amount eaten, gross energy intake, excreta energy, daily energy assimilated and apparent assimilation efficiency of Knysna and purple-crested turacos when fed artificial fruit diets of low (6.6% and 0.83 mol l^{-1}), medium (12.4% and 0.83 mol l^{-1}) and high (22% and 1.66 mol l^{-1}) glucose and sucrose concentrations

	Equicaloric (%)						Equimolar (mol l^{-1})					
	Glucose			Sucrose			Glucose			Sucrose		
	6.6	12.4	22	6.6	12.4	22	0.42	0.83	1.66	0.42	0.83	1.66
Knysna turaco												
Body mass (g)	265.1±9.8[a]	259.3±7.4[a]	258.0±7.4[a]	257.9±6.1[a]	259.1±7.7[a]	255.7±7.7[a]	265.1±9.8[a]	259.3±7.4[a]	258.0±7.4[a]	258.3±7.6[a]	258.9±8.4[a]	259.2±8.7[a]
Transit time (min)	31.0±2.8[a]	43.4±2.4[b]	44.3±1.8[b]	312.4±2.6[ab]	38.7±1.9[ab]	44.4±1[b]	31.0±2.8[a]	43.4±2.4[b]	44.3±1.8[b]	44.6±3.6[a]	65.5±5.2[b]	57.0±7.4[ab]
Amount eaten (g g^{-1} BM)	0.5±0.03[c]	0.3±0.01[a]	0.2±0.01[b]	0.4±0.03[d]	0.3±0.01[a]	0.2±0.01[b]	0.5±0.03[c]	0.3±0.01[a]	0.2±0.01[b]	0.3±0.02[a]	0.3±0.04[a]	0.2±0.01[b]
Gross energy intake (kJ g^{-1} BM)	1.3±0.1[a]	1.2±0.04[a]	0.9±0.03[b]	1.2±0.1[b]	1.1±0.03[c]	0.5±0.03[d]	1.3±0.1[a]	1.2±0.04[a]	0.9±0.03[ab]	1.2±0.1[a]	1.6±0.2[b]	1.3±0.1[a]
Excreta energy (kJ g^{-1} BM)	0.2±0.03[bc]	0.2±0.02[c]	0.1±0.02[ac]	0.3±0.03[b]	0.2±0.02[bc]	0.1±0.01[a]	0.2±0.03[bc]	0.2±0.02[c]	0.1±0.02[bc]	0.2±0.02[a]	0.2±0.02[abc]	0.1±0.01[c]
Daily energy assimilated (kJ g^{-1} BM)	1.0±0.1[a]	0.9±0.04[ab]	0.8±0.03[bcd]	0.8±0.1[ac]	0.9±0.03[ad]	0.4±0.03[e]	1.0±0.1[ab]	0.9±0.04[b]	0.8±0.03[b]	0.9±0.1[b]	1.5±0.2[a]	1.2±0.1[ab]
Apparent assimilation efficiency (%)	80.8±2.6[ab]	80.8±1.7[ab]	85.3±2.1[b]	71.5±1.5[a]	79.4±1.5[ab]	78.8±1.4[ab]	80.8±2.6[ab]	80.8±1.7[bc]	85.3±2.1[ab]	78.4±1.6[b]	89.2±1.5[ac]	92.3±0.9[a]
Purple-crested turaco												
Body mass (g)	252.6±9.4[a]	253.8±8.4[a]	252.8±7.9[a]	254.1±10.0[a]	254.2±8.0[a]	252.0±7.8[a]	252.6±9.4[ab]	253.8±8.4[a]	252.8±7.9[ab]	253.3±8.2[a]	252.5±6.4[ab]	249.0±6.1[b]
Transit time (min)	24.6±1.3[a]	27.5±4.6[acd]	36.8±3.2[bc]	20.6±1.6[a]	30.2±5.4[cd]	41.1±2.3[b]	24.6±1.3[a]	27.5±4.6[bc]	36.8±3.2[c]	35.8±4.6[bc]	49.3±3.1[d]	50.8±4.5[d]
Amount eaten (g g^{-1} BM)	0.5±0.03[c]	0.3±0.01[a]	0.2±0.01[b]	0.4±0.03[d]	0.3±0.01[a]	0.2±0.01[b]	0.5±0.03[c]	0.3±0.01[a]	0.2±0.01[ab]	0.3±0.02[a]	0.3±0.04[a]	0.2±0.01[b]
Gross energy intake (kJ g^{-1} BM)	1.3±0.1[a]	1.3±0.1[a]	1.3±0.1[a]	1.7±0.1[b]	1.2±0.1[a]	1.7±0.1[b]	1.0±0.03[b]	1.3±0.1[ab]	1.3±0.1[ab]	1.1±0.1[b]	1.0±0.1[b]	1.8±0.2[a]
Excreta energy (kJ g^{-1} BM)	0.4±0.02[a]	0.2±0.02[bc]	0.1±0.02[b]	0.5±0.1[a]	0.3±0.03[cde]	0.2±0.1[be]	0.4±0.02[a]	0.2±0.02[bc]	0.1±0.02[b]	0.4±0.1[a]	0.2±0.1[bc]	0.3±0.02[ac]
Daily energy assimilated (kJ g^{-1} BM)	0.6±0.02[b]	1.1±0.1[ab]	1.1±0.1[ab]	1.1±0.05[a]	0.9±0.04[c]	1.5±0.1[d]	0.6±0.02[b]	1.1±0.1[ab]	1.1±0.1[ab]	0.7±0.1[b]	0.7±0.04[bc]	1.5±0.2[a]
Apparent assimilation efficiency (%)	61.4±1.0[a]	82.9±0.7[a]	90.0±0.7[a]	68.5±1.7[c]	75.5±1.4[d]	88.5±2.0[a]	61.4±1.0[a]	82.9±9.7[bc]	90.0±0.7[b]	60.2±3.8[a]	77.7±5.1[cd]	82.4±2.8[bd]

BM, body mass.
Treatments with the same superscript letter are not significantly different at the 5% level.
Values are means ± s.e.m.

artificial fruit diet had the slowest transit time (50.8±4.5 min, N=5; Table 2).

Body mass

There were no significant differences in mean body mass of either Knysna turacos or purple-crested turacos when fed the six artificial equicaloric fruit diets ($F_{2,16}$=0.464, P=0.64; and $F_{2,8}$=1.64, P=0.253). Similarly, there were no significant differences in mean body mass of either Knysna turacos or purple-crested turacos when fed the six artificial equimolar fruit diets ($F_{2,16}$=0.77, P=0.481; and $F_{2,8}$=4.50, P=0.05).

Equicaloric food intake and assimilation

Knysna turacos ingested significantly different amounts of the six artificial equicaloric fruit diets ($F_{2,16}$=6.63, P=0.008; Table 2), with greater amounts of the lower-concentration diets ingested. There were significant differences between the glucose and sucrose diet treatments in terms of GEI ($F_{2,16}$=11.55, P<0.001; Table 2). There were also significant differences between the glucose and the sucrose diets in terms of energy loss in the excreta ($F_{2,16}$=3.65, P=0.049; Table 2). As a consequence of GEI and EE, DEA was significantly different for the glucose and sucrose diet treatments ($F_{2,16}$=4.56, P=0.027; Table 2). AE was low for all six diet treatments and there were no significant difference between the treatments ($F_{2,16}$=1.86, P=0.188; Table 2).

Similarly, purple-crested turacos ingested significantly different amounts of the six equicaloric artificial fruit diets ($F_{2,8}$=12.81, P=0.003; Table 2), with greater amounts of the lower-concentration diets ingested. There were significant differences between the glucose and sucrose diet treatments in terms of GEI ($F_{2,8}$=26.20, P=0.003; Table 2). There were no significant differences between the glucose and the sucrose diets in terms of energy loss in the excreta ($F_{2,8}$=0.73, P=0.509; Table 2). Again, as a consequence of GEI and EE, DEA was significantly different between the glucose and the sucrose diet treatments ($F_{2,8}$=58.90, P<0.001; Table 2). AE was low for all six diet treatments and there were significant differences between the treatments ($F_{2,8}$=19.24, P=0.0005; Table 2).

Equimolar food intake and assimilation

Knysna turacos ingested significantly different amounts of the six equimolar artificial fruit diets ($F_{2,16}$=21.06, P<0.0001; Table 2), with greater amounts of the lower-molarity diets ingested. There were no significant differences between the glucose and sucrose diet treatments in terms of GEI ($F_{2,16}$=5.03, P=0.202; Table 2). There were no significant differences between the glucose and the sucrose diets in terms of energy loss in the excreta ($F_{2,16}$=1.84, P=0.191; Table 2). As a consequence of GEI and EE, DEA was significantly different for the glucose and the sucrose diet treatments ($F_{2,16}$=5.10, P=0.020; Table 2). AE was low for all six diet treatments and there were significant differences between the treatments ($F_{2,16}$=3.96, P=0.040; Table 2).

In contrast, purple-crested turacos did not ingest significantly different amounts of the six equimolar artificial fruit diets ($F_{2,8}$=3.58, P=0.077; Table 2). There were significant differences between the glucose and sucrose diet treatments in terms of GEI ($F_{2,8}$=7.03, P=0.017; Table 2). There were also significant differences between the glucose and the sucrose diets in terms of energy loss in the excreta ($F_{2,8}$=7.23, P=0.016; Table 2). As a consequence of GEI and EE, DEA was significantly different between the glucose and the sucrose diet treatments ($F_{2,8}$=5.88, P=0.027; Table 2). AE was low for all six diet treatments but there were no significant differences between the treatments ($F_{2,8}$=1.80, P=0.227; Table 2).

DISCUSSION

Irrespective of sugar type, both Knysna and purple-crested turacos ingested greater amounts of the diets with low sugar concentrations than of the diets with high sugar concentrations. They also ingested greater amounts of the low-molarity diets at than of the high-molarity diets. These results are similar to those obtained for some other nectarivores such as sunbirds (e.g. Lotz and Nicolson, 1999; Köhler et al., 2008) and hummingbirds (e.g. López-Calleja et al., 1997). This suggests that higher intake rates of low-concentration and low-molarity diets are necessary to meet their energy requirements, as suggested by the compensatory feeding hypothesis (Simpson et al., 1989).

This emphasises the fact that when comparing food intake of different concentrations or molarities of one sugar type, energy requirements rather than preference may determine the amount eaten (Wellmann and Downs, 2009). Indeed, Knysna and purple-crested turacos maintained their mean body mass when fed on all six equicaloric artificial diet treatments and on all six equimolar artificial diet treatments indicating that they obtained adequate energy from all the treatments (Downs, 2008). The results obtained from the present study showed a higher energy intake of low equicaloric glucose concentrations than of high equicaloric sucrose concentrations for Knysna turacos, which are similar to the results of Wellman and Downs (Wellman and Downs, 2009). Interestingly, purple-crested turacos showed a higher energy intake of high equicaloric sucrose concentrations than of low equicaloric glucose concentrations.

The results obtained from the present study showed a higher energy intake of medium equimolar sucrose concentrations compared with high equimolar glucose concentrations for Knysna turacos. This suggests that they are making a choice based on sugar type rather than concentration. Interestingly, purple-crested turacos showed a higher energy intake of high equimolar sucrose concentrations than of medium equimolar sucrose concentrations. This suggests that they are making a choice based on energy levels rather than sugar type.

Apparent assimilation efficiency may be defined as how well a particular diet is digested (Witmer, 1998b). Knysna turacos showed no significant differences in AE on any of the six equicaloric artificial diets, whereas purple-crested turacos did exhibit significant differences between the equicaloric treatments. In contrast, Knysna turacos did exhibit significant differences in AE between the six equimolar artificial diet treatments, whereas purple-crested turacos showed no significant differences between the equimolar treatments. AEs in this study were lower than those obtained for typical nectarivorous species (see Martínez del Rio, 1990; Lotz and Nicolson, 1996; Jackson et al., 1998) and those obtained by Witmer for three frugivorous American thrush species (American robin *Turdus migratorius*, wood thrush *Hylocichla mustelina* and gray-cheeked thrush *Catharus minimus*) and cedar waxwing (*Bombycilla cedrorum*), which ranged from 91 to 99% (Witmer, 1999). Worthington also found high assimilation efficiencies, ranging from 86 to 97.6% in two manakin species (*Manacus vitellinus* and *Pipra mentalis*) (Worthington, 1989). Our results are more consistent with those for Cape white-eyes (*Zosterops virens*) obtained by Wellmann and Downs who found apparent assimilation efficiencies of 79.3–85.6% on artificial equicaloric glucose fruit and 69.0–78.4% on artificial equicaloric sucrose fruit (Wellmann and Downs, 2009).

When food is allowed to stay in the gut for a longer period there may be an increase in the absorption of nutrients (Klasing, 1998). Digestive transit times therefore may indicate how well nutrients are absorbed by the gut (Witmer, 1998a). For both turaco species,

digesta transit times increased with increasing concentration and molarity for the glucose and the sucrose artificial diets. Although both species experienced the slowest digesta transit times on high equicaloric sucrose concentrations, digesta transit times were the shortest on low equicaloric concentrations of glucose for Knysna turacos and low equicaloric concentrations of sucrose for purple-crested turacos. Digesta transit times for the equimolar artificial diets were the slowest on medium sucrose molarity and high sucrose molarity for Knysna and purple-crested turacos, respectively. Both species experienced the shortest digesta transit times on the low glucose molarity diets. These results are similar to those of Wellman and Downs (Wellmann and Downs, 2009) who found similar trends for a glucose equicaloric artificial diet. However, digesta transit times were measured on fasted birds and may therefore not be representative of typical digesta transit times because birds usually have food in their gut (Levey and Martínez del Rio, 1999).

Knysna turacos ingested more of the low equicaloric glucose diet whereas purple-crested turacos ingested more of the low equicaloric sucrose diet, and these diets had the shortest digesta transit times in each species, respectively. Similarly, both Knysna and purple-crested turacos ingested more of the low equimolar glucose diet and this diet had the shortest digesta transit times in both species. Similar results were obtained by Witmer, who suggested that birds would have to have a higher intake of dilute food (than of more concentrated food) to increase energy intake and to meet energy requirements, because these foods would be processed more swiftly through the gut (Witmer, 1998a). Witmer also suggested that birds may be able to compensate for low sugar concentration by being able to process low sugar fruits more swiftly. This has disadvantages in that more time would then be required to find, ingest and digest these fruits (Witmer, 1998a).

Our results show that both turaco species had slower digesta transit times as concentration and molarity of the food increased; and suggest that both turaco species would be able to subsist on either sucrose- or glucose-rich fruits as, regardless of sugar type, both species were able to maintain body mass on all six artificial fruit diets. Our results also show that both turaco species were able to regulate their energy intake, with higher intake rates occurring on more dilute sugar concentrations, and although apparent assimilation efficiencies obtained for both turaco species were lower than for most nectar and fruit eating studies they still fell within the range of published examples. Consequently our predictions are supported.

In summary, these two frugivores appear to be tolerant of sugar type. Future studies looking at the sugars in indigenous forest fruits may give insight into food preferences of the turaco species and their role as potential seed dispersers of fruiting tree species.

LIST OF SYMBOLS AND ABBREVIATIONS

AE	apparent energy assimilation efficiency
DEA	daily energy assimilated
DFI	daily food intake
EE	excreta energy loss
GEI	gross energy intake

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