

Food preferences of Knysna and purple-crested turacos fed varying concentrations of equicaloric and equimolar artificial fruit

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Accepted 27 October 2010

SUMMARY

The effects that different fruit sugar types and concentrations have on food preferences of avian frugivores have been relatively poorly studied. Although it has been recently advocated that preference is based on equicaloric energy it is also important to note whether preferences change as energy content changes. Therefore, sugar preferences of equicaloric and equimolar artificial fruit of different sugar types at varying concentrations and molarities were investigated in two relatively large South African frugivores, Knysna (*Tauraco corythaix*) and purple-crested (*Gallirex porphyreolophus*) turacos. Artificial fruits containing 6.6, 12.4 or 22% sucrose or glucose, and artificial fruits containing 0.42, 0.83 or 1.66 mol l⁻¹ sucrose or glucose, were used to determine sugar preferences. Knysna turacos preferred the sucrose to the glucose equicaloric artificial fruit diet at low concentrations whereas purple-crested turacos showed no preference for either diet. Both turacos species preferred the sucrose equimolar artificial fruit diet to the glucose at low concentrations. At high concentrations neither species showed a preference for either equicaloric or equimolar artificial fruit diets. This suggests that energy requirements influence food preferences more than sugar type and that birds will select fruit that is higher in energy irrespective of sugar type. This complements an earlier study on digestion of differing equicaloric and equimolar artificial fruit sugar types. It again emphasizes the need for future studies looking at the composition of indigenous forest fruit sugars in order to obtain insight into the role of these avian frugivores as potential seed dispersers of fruiting tree species.

Key words: sugar type, sugar preference, energy requirement, frugivory, Knysna turaco, purple-crested turaco, artificial fruit.

INTRODUCTION

Many animal species show preferences for certain food types (Ayala-Berdon et al., 2008). The amount of food consumed by the animal is usually reduced as levels of available energy are increased (Collins, 1981; Slansky and Wheeler, 1992). Studies of this 'intake response' (Castle and Wunder, 1995) have mostly focused on nectarivorous birds (Collins, 1981; López-Calleja et al., 1997; McWhorter and Martínez del Rio, 2000) but these issues have seldom been addressed in frugivores (see Levey and Martínez del Rio, 1999).

According to Baker and Baker, hummingbird-pollinated plants produce nectar that is rich in sucrose, whereas passerine-pollinated plants produce nectar in which hexose sugars are dominant (Baker and Baker, 1983). Some choice tests have shown that several hummingbird species prefer sucrose to glucose or fructose (Hainsworth and Wolf, 1976; Martínez del Rio, 1990a), whereas some passerine species prefer glucose and fructose to sucrose (Martínez del Rio and Stevens, 1989; Martínez del Rio et al., 1989). However, Lotz and Schondube suggested that birds will generally prefer hexose sugars to sucrose at low equicaloric concentrations but will prefer sucrose to hexose at high equicaloric concentrations (Lotz and Schondube, 2006). A possible explanation for this switch at high concentrations is that sucrose nectar contains double the energy content per unit of osmotic concentration than hexose nectar (Beuchat et al., 1990). This reduced osmotic concentration may increase post-ingestional intestinal energy delivery rate by increasing gastric emptying rate (Karasov and Cork, 1994; Schondube and Martínez del Rio, 2003). If the delivery of high osmotic, concentrated solutions is not regulated birds may

experience osmotic diarrhoea (Lotz and Schondube, 2006). Sucrotic birds may therefore lessen their osmotic stress by choosing sucrose rather than hexose at high concentrations but at low concentrations this effect may have less consequence (Lotz and Schondube, 2006). However, Johnson and Nicolson recommend that a more useful distinction would be between specialist and generalist bird pollination systems (Johnson and Nicolson, 2008). They suggest that generalist bird-pollinated plants are characterised by large volumes of nectar (probably as a result of occasional avian nectarivores having a much large body size) with low concentrations and low sucrose proportions whereas specialist bird-pollinated plants are characterised by smaller volumes of nectar with higher concentrations and high sucrose proportions. It has also been suggested that preferences are based on energy yield for relatively small specialist nectarivores (Downs and Perrin, 1996).

However, experimental procedure may affect the results of choice tests (Brown et al., 2008). Previous studies have used solutions that are equicaloric (Fleming et al., 2004), equimolar (Downs, 1997; Downs, 2000) or solutions that are equivalent by mass (Lotz and Nicolson, 1996; Blem et al., 2000). Equimolar solutions offer equal amounts of molecules per solution, but a sucrose solution at a particular concentration has approximately double the energy of an equimolar hexose solution (Hixon, 1980; Schoener, 1983; Downs and Perrin, 1996; Downs, 1997). Sucrose solutions that are equivalent in sugar mass to a hexose sugar solution have approximately 5% more available energy (Fleming et al., 2004). It has therefore been suggested that in choice tests sugar solutions that are energetically equivalent should be used (Fleming et al., 2004).

Most non-passerine frugivorous birds (e.g. pigeons, hornbills, trogons and turacos) (Snow, 1981; Levey and Martínez del Rio, 2001; Lotz and Schondube, 2006) have been poorly studied with regards to the sugar content of fruits that they consume. Musophagiformes members play a key role in plant reproduction, as seed dispersal agents (Herrera, 2002), because the order consists exclusively of frugivores (Kissling et al., 2009). The preferences for different sugar types at varying concentrations and molarities were therefore investigated in two non-passerine, relatively large avian frugivores, Knysna (*Tauraco corythaix* Wagler 1827) and purple-crested (*Gallirex porphyreolophus* Vigors 1831) turaco (Musophagiformes: Musophagidae). Both Knysna (ca. 310 g) and purple-crested turacos (ca. 300 g) are forest frugivores (Rowan, 1983; Oatley, 1997; du Plessis and Dean, 2005a; du Plessis and Dean, 2005b).

The aim of the study was to determine if food preference was affected by sugar type and concentration. Initially equicaloric artificial fruit were used; however, to show the possible importance of energy in foraging decisions the experiments were repeated using equimolar artificial fruit. It was hypothesised that sugar type and concentration would affect food preferences in the two species of turacos. It was predicted that both species would: (1) show no preference for either equicaloric glucose or equicaloric sucrose irrespective of concentration, and (2) would show a preference for equimolar sucrose to equimolar glucose, because of the differences in energy yields.

MATERIALS AND METHODS

Bird capture and maintenance

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

Food choice experiments

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

Food preferences (determined by the intake rates) of sucrose and glucose diet treatments were investigated for both equicaloric and equimolar artificial diets at low (6.6% and 0.42 mol l⁻¹, respectively) and high (22% and 1.66 mol l⁻¹, respectively) concentrations and molarities. Artificial fruits were made by mixing all the relevant ingredients (see Table 1 for the composition of equicaloric artificial fruit diets and Table 2 for the composition of equimolar artificial fruit diets) into 1 litre of boiling water (Witmer, 1998). The mixture was then stirred continuously to ensure that the ingredients were

Table 1. Summary of experimental treatments for equicaloric food choice tests

Treatment	Tray A	Tray B
	Sugar type and concentration	Sugar type and concentration
Trial 1	Low sucrose	Low glucose
Trial 2	High sucrose	High glucose
Control 1	Medium sucrose	Medium sucrose
Control 2	Medium glucose	Medium glucose

Table 2. Summary of experimental treatments for equimolar food choice tests

Treatment	Tray A	Tray B
	Sugar type and molarity	Sugar type and molarity
Trial 1	Low sucrose	Low glucose
Trial 2	High sucrose	High glucose
Control 1	Medium sucrose	Medium sucrose
Control 2	Medium glucose	Medium glucose

dispersed evenly while it solidified. Once the mixture had hardened the artificial fruit was cut into approximately 1×1×1 cm cubes to ensure that the birds could swallow the fruits whole. All dietary treatments were analysed for energy content using a bomb calorimeter (Animal Science, University of KwaZulu-Natal, South Africa). The sample was placed in the bomb and oxygen was then admitted under pressure. The water temperature in the bomb calorimeter was recorded and then the sample was ignited electrically. The water temperature was recorded again once equilibrium had been reached. The temperature rise and the specific heats and masses of the water and the bomb were used to calculate the quantity of the heat produced (McDonald et al., 1995).

On the experimental day, the body mass (g) of the birds was measured at 06:00 h (30–40 min prior to the light phase) and 18:00 h to the nearest 0.5 g using a digital scale (Adam[®], Durban, KwaZulu-Natal, South Africa) and birds were each provided with a set amount of weighed food (measured to 0.01 g) of each diet treatment. The food trays were placed on opposite sides of the cage with a perch halfway between the trays. To ensure that no depletion effects occurred, each bird was provided with sufficient food of each diet treatment than could be eaten by a bird on a given day. Experiments were run for 12 h (from 06:00 h to 18:00 h). Tables 1 and 2 summarise the trials conducted on individuals of each species for both equicaloric and equimolar food choice experiments, respectively. For half of the birds, food tray A was placed on the right-hand side of the cage and tray B on the left-hand side, and *vice versa* for the remainder of the birds, in order to avoid possible spatial bias. Separate medium sucrose and medium glucose trials (see Tables 1 and 2) were run in order to test for possible spatial bias. Evaporative moisture loss from the uneaten food was estimated using controls of each experimental artificial diet. The maintenance diet was fed to the birds between experiments and each specific experimental diet was incorporated into the maintenance diet 1 day prior to that experiment being conducted. The birds were not fed the artificial diet on any two consecutive days.

For each bird, hourly intake rates and overall daily food intake (DFI; measured as wet mass) of each diet treatment were determined. These were quantified by subtracting the mass of the food left over from the amount given. Evaporative water loss was taken into account. 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. Finally the data were converted to per gram individual body mass by dividing by the mean of initial and final body mass on the day of experimentation for comparisons. The above protocol was repeated for each bird species and each diet treatment.

Analyses

As the same birds were used repeatedly, food preference was 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

Body mass

Body mass of Knysna turacos ranged from 259.31±7.35 g to 260.28±9.05 g when fed the glucose 12.4% control and the glucose and sucrose 6.6% experimental diet, respectively; and from 257.89±8.74 g to 261.06±8.17 g when fed the glucose and sucrose 1.66 mol l⁻¹ experimental diet and the glucose and sucrose 0.42 mol l⁻¹ experimental diet, respectively.

Body mass of purple-crested turacos ranged from 248.30±7.47 g to 254.40±8.07 g when fed the glucose and sucrose 6.6% experimental diet and the sucrose 12.4% control diet, respectively; and from 248.20±6.45 g to 254.00±8.36 g when fed the glucose and sucrose 0.42 mol l⁻¹ experimental diet and the glucose 0.83 mol l⁻¹ control diet.

Equicaloric food preference

Knysna turacos did not exhibit any side bias for either equicaloric glucose or sucrose ($F_{1,8}=0.98, P=0.352; F_{1,8}=7.96, P=0.225$, respectively). Similarly, purple-crested turacos also did not exhibit any side bias for either equicaloric glucose or sucrose ($F_{1,4}=2.91, P=0.163; F_{1,4}=12.20, P=0.251$, respectively).

In terms of hourly intake rates, Knysna turacos significantly preferred the 6.6% sucrose to the 6.6% glucose artificial fruit diet ($F_{11,88}=3.16, P=0.001$) and they consistently ingested more of the 6.6% sucrose artificial fruit diet every hour over a 12 h period (Fig. 1A). In contrast, purple-crested turacos did not significantly prefer the 6.6% sucrose to the 6.6% glucose artificial fruit diet ($F_{11,44}=1.73, P=0.098$; Fig. 1B).

Knysna turacos ingested significantly different total amounts of the two 6.6% artificial diet treatments and there was a significant difference between the two 6.6% treatments in terms of GEI (Table 3). In contrast, there was no significant difference between

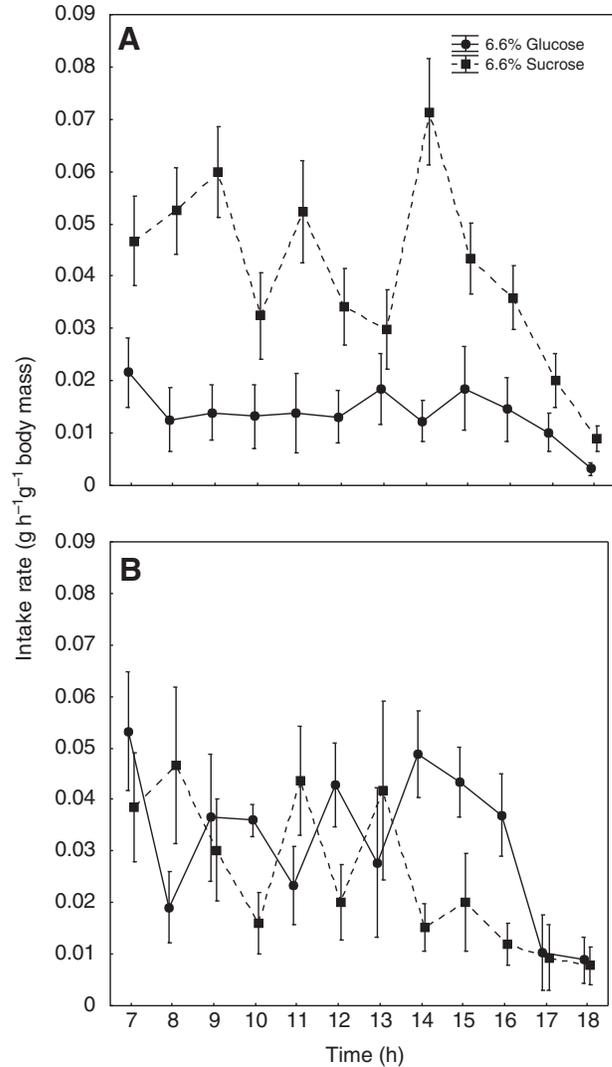


Fig. 1. Amount of the glucose (circles) and sucrose (squares) 6.6% artificial diets eaten per hour by (A) Knysna turacos and (B) purple-crested turacos. Values are means ± s.e.m.

the total amounts of the two 6.6% treatments eaten by purple-crested turacos and there was no significant difference between the treatments in terms of GEI (Table 3).

Table 3. Total amount eaten and gross energy intake of each artificial fruit diet by Knysna and Purple-crested turacos during the choice experiments

Treatment	Total amount eaten (g g ⁻¹ BM)					GEI (kJ g ⁻¹ BM)				
	Sucrose	Glucose	F	P	N	Sucrose	Glucose	F	P	N
Knysna turacos										
6.6%	0.4±0.1	0.1±0.03	9.35	0.016	9	1.0±0.1	0.3±0.1	10.49	0.012	9
22%	0.2±0.03	0.1±0.2	2.74	0.136	9	0.5±0.1	0.7±0.2	0.37	0.562	9
0.42 mol l ⁻¹	0.2±0.02	0.1±0.02	21.24	0.002	9	1.0±0.1	0.1±0.1	48.62	<0.001	9
1.66 mol l ⁻¹	0.1±0.03	0.1±0.03	0.72	0.421	9	1.1±0.2	0.5±0.2	2.23	0.174	9
Purple-crested turacos										
6.6%	0.2±0.04	0.2±0.03	0.36	0.58	5	0.7±0.1	0.7±0.1	0.01	0.928	5
22%	0.2±0.02	0.1±0.03	0.58	0.49	5	1.1±0.2	0.7±0.2	1.48	0.291	5
0.42 mol l ⁻¹	0.3±0.02	0.1±0.01	57.12	0.002	5	0.9±0.1	0.3±0.02	66.48	0.001	5
1.66 mol l ⁻¹	0.1±0.001	0.1±0.01	1.51	0.286	5	0.9±0.1	0.6±0.1	11.49	0.028	5

BM, body mass.

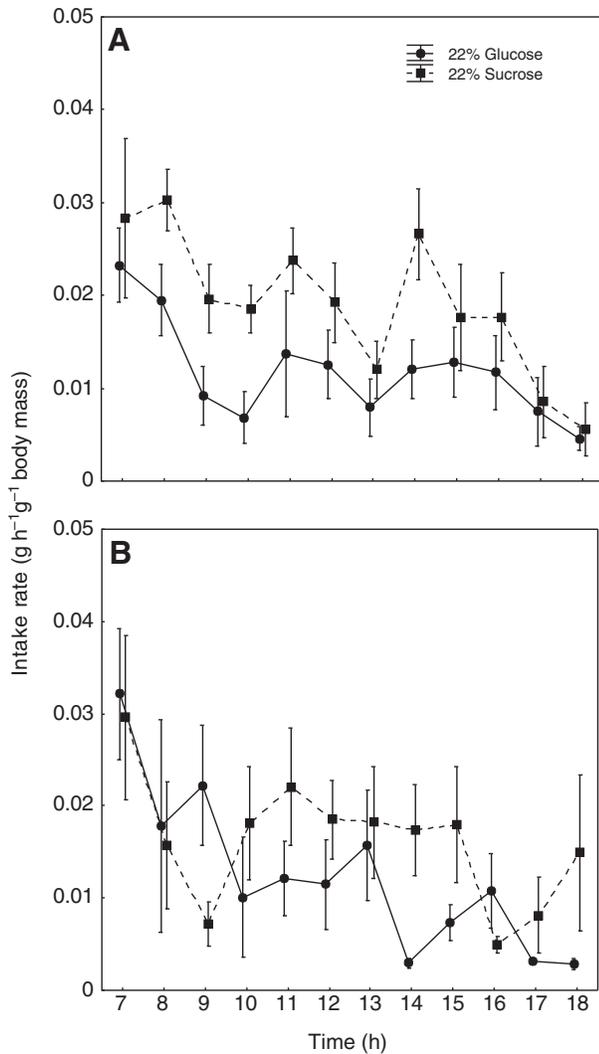


Fig. 2. Amount of the glucose (circles) and sucrose (squares) 22% artificial fruit diet eaten per hour by (A) Knysna turacos and (B) purple-crested turacos. Values are means \pm s.e.m.

In terms of hourly intake rates of high concentrations, Knysna turacos did not significantly prefer the 22% sucrose to the 22% glucose artificial fruit diet ($F_{11,88}=0.61$, $P=0.815$; Fig. 2A). Similarly, purple-crested turacos did not significantly prefer the 22% sucrose to the 22% glucose artificial fruit diet ($F_{11,44}=0.93$, $P=0.518$; Fig. 2B).

There were no significant differences between the total amounts eaten of the 22% diet treatments by either Knysna or purple-crested turacos, and for both species there were no significant differences between the two 22% treatments in terms of GEI (Table 3).

Equimolar food preference

Knysna turacos did not exhibit any side bias for either equimolar glucose or sucrose ($F_{1,8}=0.97$, $P=0.352$; $F_{1,8}=6.05$, $P=0.393$, respectively). Similarly, purple-crested turacos also did not exhibit any side bias for either equicaloric glucose or sucrose ($F_{1,4}=0.24$, $P=0.648$; $F_{1,4}=1.07$, $P=0.359$, respectively).

In terms of hourly intake rates, of the lower concentrations, Knysna turacos did not significantly prefer the 0.42 mol l⁻¹ sucrose to the 0.42 mol l⁻¹ glucose artificial fruit diet ($F_{11,88}=1.16$, $P=0.330$;

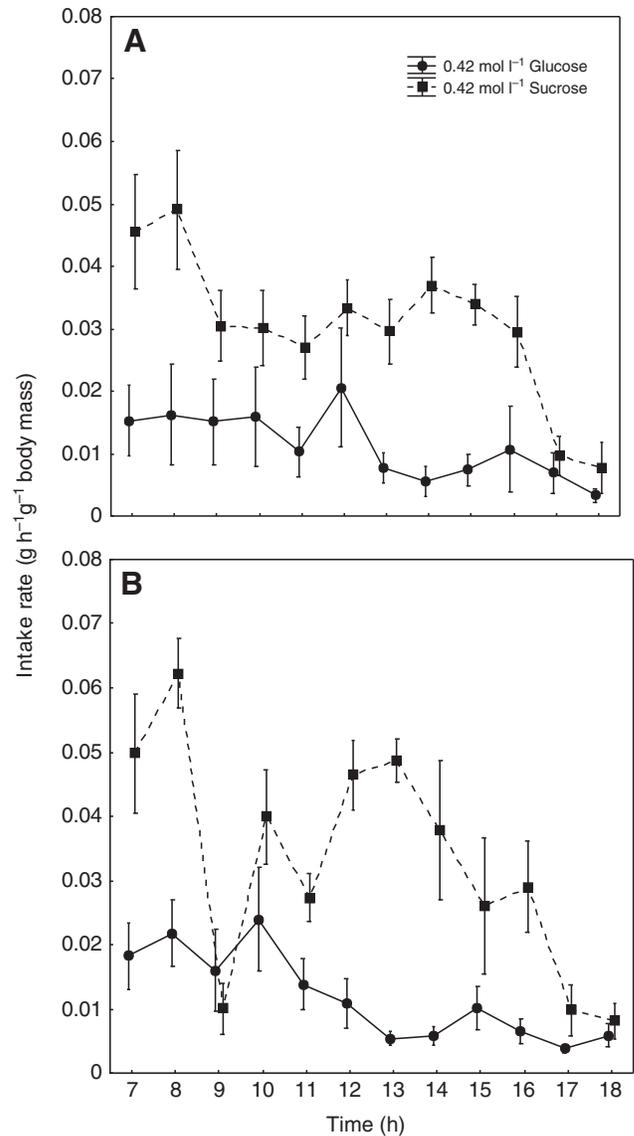


Fig. 3. Amount of the glucose (circles) and sucrose (squares) 0.42 mol l⁻¹ artificial diet eaten (mean \pm s.e.m.) per hour by (A) Knysna turacos and (B) purple-crested turacos. Values are means \pm s.e.m.

Fig. 3A). In contrast, purple-crested turacos significantly preferred the 0.42 mol l⁻¹ sucrose to the 0.42 mol l⁻¹ glucose artificial fruit diet ($F_{11,44}=3.15$, $P=0.003$; Fig. 3B).

Knysna and purple-crested turacos both ingested significantly different total amounts of the two 0.42 mol l⁻¹ artificial diet treatments and there was a significant difference between the two 0.42 mol l⁻¹ treatments in terms of GEI (Table 3).

In terms of hourly intake rates of the high concentrations, Knysna turacos did not significantly prefer the 1.66 mol l⁻¹ sucrose to the 1.66 mol l⁻¹ glucose artificial fruit diet ($F_{11,88}=0.80$, $P=0.634$; Fig. 4A). Similarly, purple-crested turacos did not significantly prefer the 1.66 mol l⁻¹ sucrose to the 1.66 mol l⁻¹ glucose artificial fruit diet ($F_{11,44}=1.31$, $P=0.247$; Fig. 4B).

There were no significant differences between the total amounts of the two 1.66 mol l⁻¹ artificial diet treatments eaten by both Knysna and purple-crested turacos (Table 3). For Knysna turacos there was no significant difference between the two 1.66 mol l⁻¹ treatments in

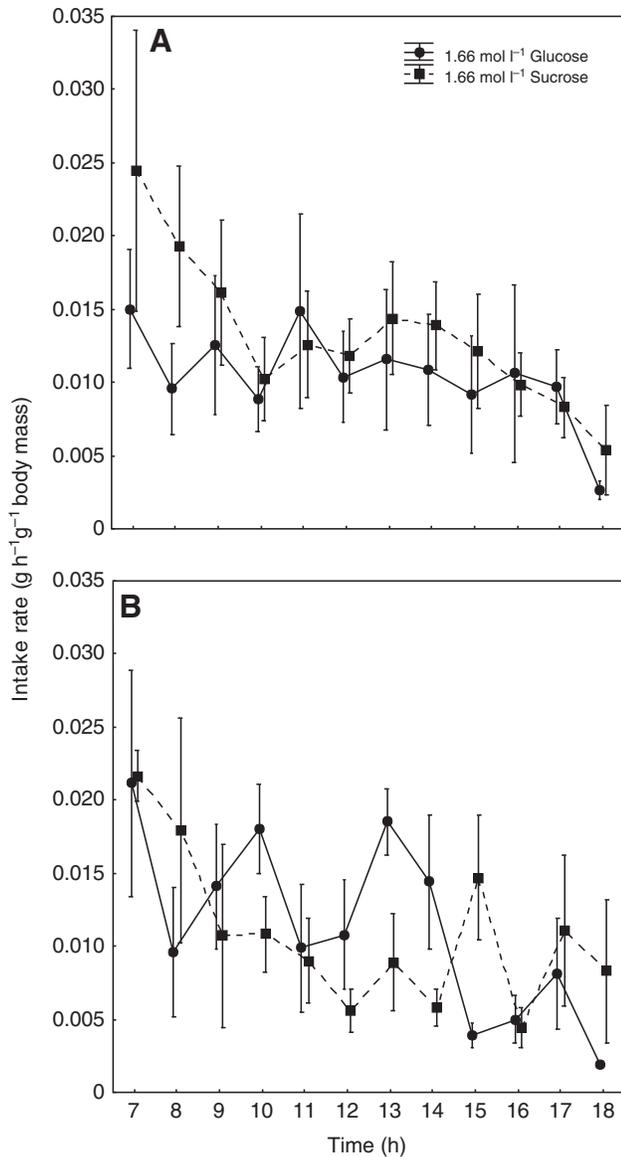


Fig. 4. Amount of the glucose (circles) and sucrose (squares) 1.66 mol l^{-1} artificial diet eaten (mean \pm s.e.m.) per hour by (A) Knysna turacos and (B) purple-crested turacos. Values are means \pm s.e.m.

terms of GEI (Table 3). In contrast, for purple-crested turacos there was a significant difference between the two 1.66 mol l^{-1} treatments in terms of GEI (Table 3).

DISCUSSION

These relatively large frugivorous birds generally had higher food intake rates in the mornings with intake rates decreasing as the day progressed, irrespective of sugar type. This is probably as a result of them having a relatively large ventriculus, which allows a greater initial food intake (Wilson, 2009). This also shows that birds increase their food intake initially to achieve their energy requirements.

Knysna turacos preferred the sucrose to glucose equicaloric artificial fruit diet at low concentrations whereas purple-crested turacos showed no preference for either diet. In contrast, purple-crested turacos preferred the sucrose equimolar artificial fruit diet to the glucose one at low concentrations, whereas Knysna turacos

showed no preference for either fruit diet. At high concentrations neither species showed a preference for either sugar in equicaloric or equimolar artificial fruit diets. These results for equicaloric diets differ from those obtained for some nectarivores such as white-bellied sunbirds (*Cinnyris talatala*) (Fleming et al., 2004), cinnamon-bellied flowerpiercers (*Diglossa baritula*) and magnificent hummingbirds (*Eugenes fulgens*) (Schondube and Martínez del Rio, 2003), New Holland honeyeaters (*Phylidonyris novaehollandiae*), rainbow lorikeets (*Trichoglossus haematotus*) and red rattlebirds (*Anthochaera carunculata*) (Fleming et al., 2008), which preferred hexose sugars at low concentrations and sucrose at high concentrations. However, our results are similar to those obtained by Stiles who found that, in choice tests, four species of hummingbirds (*Calypte anna*, *Selasphorus rufus*, *Archilocus alexandri* and *Thalurania furcata*) all preferred sucrose over equicaloric glucose (Stiles, 1976). In their studies Hainsworth and Wolf and Martínez del Rio also found that hummingbird species prefer sucrose over glucose or fructose (Hainsworth and Wolf, 1976; Martínez del Rio, 1990b). Our results also correspond to those of Downs and Perrin who found that three nectarivorous birds species (Gurney's sugarbird *Promerops gurneyi*, malachite sunbird *Nectarinia famosa* and black sunbird *Nectarinia amethystina*) all preferred sucrose at low equimolar concentrations, and showed no preference at high equimolar concentrations (Downs and Perrin, 1996). Downs and Perrin suggest that energy rewards may play less of a role as sugar concentrations increase and therefore the birds may not exhibit a preference for either sugar at high concentrations (Lloyd, 1989; Stromberg and Johnson, 1990). In the present study this preference for energy yield would not apply for the equicaloric artificial fruits because the energy yield for sucrose and glucose at a particular concentration should be equal. The preference results obtained in this study support this idea. Although Knysna turacos showed no significant preference for equimolar sucrose over equimolar glucose at low molarity, which would have been expected in terms of energy rewards (see Downs and Perrin, 1996; Downs, 1997), they ingested more sucrose than glucose in total.

Our results showed that Knysna turacos preferred sucrose to glucose equicaloric artificial fruit diet at low concentrations, whereas purple-crested turacos had no preference for either diet, and at high equicaloric concentrations neither species displayed a preference for either sugar. Our results also showed that although purple-crested turacos preferred sucrose to glucose equimolar artificial fruit diet at low concentrations, Knysna turacos had no preference for either sugar type, and at high equimolar concentrations neither species displayed a preference for either sugar. We therefore reject our predictions.

The result of this study concurs with the conclusions obtained in a previous study (see Wilson and Downs, 2011). Both Knysna and purple-crested turacos are able to subsist on fruits that are rich in either sucrose or glucose but further studies of the sugar composition in indigenous fruits are needed in order to obtain insight into the role of avian frugivores as seed dispersers.

ACKNOWLEDGEMENTS

A.-L.W. would like to thank the National Research Foundation and the Gay Langmuir bursary fund for financial assistance. We thank Rob Poley for kindly lending us his purple-crested turaco; Adam Shuttleworth for his valuable advice, proofreading and assistance with data collection; Mark Brown for his valuable advice and assistance for caring for the turacos; the Animal House and Thami Mjwara for housing and caring for the turacos; Siyabonga Madlala, Ebrahim Ally and Lorinda Jordaan for assistance with data collection; and Douglas Levey and Katrin Böhning-Gaese and an anonymous reviewer for their valuable comments. Ethical clearance for this study has been approved by the Animal Ethics sub-committee of the University of KwaZulu-Natal.

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