

Sugar preferences and digestive efficiency of the village weaver: a generalist avian pollinator of African plants

T. C. Odendaal, M. Brown*, C. T. Downs and S. D. Johnson

School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, South Africa

*Author for correspondence (brownma@ukzn.ac.za)

Accepted 6 April 2010

SUMMARY

Recent research has shown that nectar properties of flowers pollinated by generalist avian nectarivores differ markedly from those of flowers pollinated by specialist avian nectarivores. In particular, flowers pollinated by generalist avian nectarivores tend to have very dilute nectar dominated by hexose sugars. To establish whether pollinator-mediated selection can explain these traits, we tested nectar sugar preferences and digestive capabilities of the village weaver (*Ploceus cucullatus*), a common generalist passerine nectarivore in South Africa. When offered pairwise choices of equicaloric hexose and sucrose solutions, village weavers preferred hexose solutions at 5% and 10% sucrose equivalents (SE) but did not show significant preference for either type of sugar when higher concentrations were offered (15%, 20% and 25% SE). Birds were less efficient at absorbing sucrose than hexose sugars, as revealed by high-performance liquid chromatography (HPLC) analysis of excreta sugar content. This was true at both concentrations tested (8.22% and 25%), although apparent sucrose assimilation rates were still relatively high ($89.6 \pm 2.9\%$ at low concentrations and $93.6 \pm 1.7\%$ at high concentrations). Transit times indicated that sucrose also passes through the digestive tract faster than hexose sugars, particularly when consumed at high concentrations. This may limit the rate at which sucrose can be hydrolyzed before absorption. These results indicate that hexose preferences in generalist avian nectarivores may help explain the low sucrose content in flowers pollinated by these birds. Moreover, the preference for hexose sugars in weavers was most evident at the low concentrations (ca. 9% sugar by mass) that are typical of nectar in flowers pollinated by generalist avian nectarivores.

Key words: apparent absorption efficiency, sucrose, hexose, transit time, *Ploceus cucullatus*.

INTRODUCTION

Earlier literature on bird pollination systems emphasized a dichotomy in nectar properties between hummingbird (Apodiformes: Trochilidae) and passerine (Passeriformes) systems (Cruden and Toledo, 1977; Baker and Baker, 1983). More specifically, hummingbird-pollinated plants were shown to have sucrose-rich nectar, while passerine-pollinated plants were found to have hexose-rich nectars (Baker and Baker, 1983). Initial research into sugar preferences of these two groups of birds found that hummingbirds preferred sucrose solutions (Stiles, 1976; Hainsworth and Wolf, 1976; Martínez del Río, 1990; Martínez del Río et al., 1992) and passerines preferred hexose solutions, and indeed in several cases passerines were shown to be sucrose intolerant (Martínez del Río et al., 1988; Martínez del Río et al., 1992; Martínez del Río and Stevens, 1989; Martínez del Río, 1990; Brugger and Nelms, 1991; Brugger et al., 1993).

However, recent research has shown that not only are nectar properties in flowers pollinated by specialized passerines strongly convergent with those of hummingbird-pollinated flowers (Johnson and Nicolson, 2008) but that they too show preferences for sucrose-rich solutions (Downs and Perrin, 1996; Lotz and Nicolson, 1996; Jackson et al., 1998a; Jackson et al., 1998b). By contrast, plants pollinated by generalist avian nectarivores [also referred to as 'occasional nectarivores' because they often utilize nectar only as a secondary food source (cf. Johnson et al., 2006)] tend to produce a higher volume of nectar, with a lower sugar concentration and a lower proportion of sucrose, than do plants pollinated by specialist avian nectarivores (Johnson and Nicolson, 2008; Brown et al., 2009;

Symes et al., 2009). Specifically, Johnson and Nicolson found that plants pollinated by specialist nectarivores are characterized by low (10–30 µl) volumes of relatively concentrated (15–25% w/w) sucrose-rich (40–60% of total sugar) nectars while plants pollinated by occasional bird pollinators are characterized by large volumes (40–100 µl) of very dilute (8–12%) nectar, with low (0–5%) sucrose content (Johnson and Nicolson, 2008). In the Americas, this distinction fits the classic hummingbird–passerine dichotomy (Cruden and Toledo, 1977). However, in Africa, where hummingbirds do not occur, this dichotomy applies to passerine-pollinated plants, raising the interesting possibility that generalized and specialized passerine nectarivores differ in their nectar preferences.

It has long been suggested that pollinator preference drives selection on nectar rewards (Wykes, 1952; Martínez del Río et al., 1992), and hence preference experiments have been conducted quite extensively on specialist nectarivorous birds (Downs and Perrin, 1996; Lotz and Nicolson, 1996; Roberts, 1996; Downs, 1997a; Jackson et al., 1998a; Jackson et al., 1998b; Schondube and Martínez del Río, 2003; Fleming et al., 2004; Lotz and Schondube, 2006). These studies indicate that specialized passerines such as sunbirds have sugar preferences and digestive capacities that are similar to those of hummingbirds (Fleming et al., 2004; Lotz and Schondube, 2006). Most specialized avian nectarivores exhibit either a preference for sucrose, or no preference at high concentrations, no preference at intermediate concentrations, and switch to a hexose preference at low concentrations (Fleming et al., 2004; Fleming et al., 2008; Brown et al., 2010a). However, these switches to hexose

preference generally occur at very low concentrations (<10%) that are not found naturally in flowers pollinated by these birds, and may therefore not be biologically relevant to selection on nectar traits (Brown et al., 2010a).

Primary causes of the concentration-dependent preferences in specialists are suggested by authors to be elements of digestive physiology, specifically: (1) accommodation of high osmotic concentrations when birds consume concentrated hexose; and (2) sucrose hydrolysis rate limitations when large volumes of dilute solutions are consumed (Martínez del Río et al., 2001; Fleming et al., 2004; Lotz and Schondube, 2006).

Sugar preference experiments have been conducted on a number of generalist avian nectarivores species. These can be divided into those concerned only with members of the Muscicapidae superfamily, lacking sucrase activity (Schuler, 1983; Martínez del Río and Stevens, 1989; Brugger, 1992; Malcarney et al., 1994; Gatica et al., 2006), and those concerned with other species (Martínez del Río et al., 1989; Franke et al., 1997; Lane, 1997; Mata and Bosque, 2004; Brown et al., 2010b). From the latter group, it is evident that generalist avian nectarivores, although they possess some ability to digest sucrose, prefer hexose sugars. However, apart from recent work on bulbuls by Brown et al. (Brown et al., 2010b), only comparisons at single concentrations have been reported, and these concentrations have not been representative of the very dilute nectar found in flowers pollinated by these birds. Also, test solutions in earlier studies were not equicaloric; thus, conflating tests of sugar preference with an energy difference between test solutions (Brown et al., 2008).

The avoidance of sucrose, particularly by members of the Muscicapidae superfamily, has been shown to be the consequence of a limited activity (Martínez del Río et al., 1988; Martínez del Río et al., 1989) or a complete lack (Martínez del Río and Stevens, 1989) of the digestive enzyme sucrase, necessary for the hydrolysis and subsequent assimilation of this sugar. If such a physiological constraint was a general trend among occasional nectarivores, then hexose preference would be expected. Because specialist nectarivore preferences do not adequately explain the low proportion of sucrose and dilute nature of some nectars (Fleming et al., 2004; Brown et al., 2010a), it has been suggested that preferences of occasional nectarivores may be a contributing factor to selection for nectar sugars (Dupont et al., 2004; Fleming et al., 2004; Brown et al., 2010b). Johnson and Nicolson propose that a better understanding of foraging preferences and digestive abilities of occasional nectarivores is important to explain why nectars of generalist bird-pollinated plants are hexose rich (Johnson and Nicolson, 2008).

The aim of this study was to establish whether pollinator-mediated selection can explain the dominance of hexose sugars in the dilute nectar of plants pollinated by generalist avian nectarivores. The village weaver *Ploceus cucullatus* Müller was studied, as this species and several other closely related weavers are important pollinators of plants with flowers adapted to short-billed generalist avian nectarivores (Oatley and Skead, 1972; Daniels, 1987; Botes et al., 2008; Symes et al., 2008; Brown et al., 2009). Village weavers are predominantly granivores but feed on nectar opportunistically throughout of the year. It was predicted that this generalist nectarivore would have a preference for hexose sugars, and that this preference would be more pronounced when it was offered dilute solutions that approximate the concentration of nectar in flowers pollinated by this bird. Because sugar preference may be determined by digestive efficiency, apparent absorption efficiencies and transit times of nectar sugars were also determined. It was predicted that hexose sugars would pass through the digestive tract more slowly

and, hence, together with possible limitations of sucrase activity, be absorbed more efficiently.

MATERIALS AND METHODS

Capture and maintenance of village weavers

Ten non-breeding adult village weavers were captured using mistnets (May 2007) at Hilton College, outside Pietermaritzburg, South Africa (29°36'S 30°26'E), under license from the local conservation authority Ezemvelo KwaZulu-Natal Wildlife. The birds were held in outdoor aviaries (4.2 m × 2 m × 1 m) at the University of KwaZulu-Natal Animal House, Pietermaritzburg Campus for ca. three weeks before being moved indoors for the trials. They were fed a maintenance diet of mixed bird seed (*Panicum miliaceum* and *Panicum maximum*), mixed nectar ± 20% [1:1 sucrose and hexose (equal fructose and glucose) w/w], bonemeal (protein source) with water *ad libitum*. Bird mass (36.7 ± 0.9 g mean ± s.e.) was representative of the species in the capture area (38.0 ± 0.1 g; *N* = 1338) (M.B., unpublished data).

All birds were transferred to individual indoor (25°C with a 12 h:12 h L:D) experimental cages (90 cm × 30 cm × 45 cm), and restricted to one half of the cage during experiments. No food or water was available to them overnight before a trial, so as to ensure a post-absorptive state. Each bird had at least two days on the maintenance diet and water between trials. Trials were conducted during June to July.

Sugar preference

Equicaloric sucrose and hexose (1:1 fructose and glucose) nectars were offered simultaneously to individual birds at five concentrations, 5%, 10%, 15%, 20% and 25% sucrose equivalents (SE). The low concentrations (5% and 10%) are similar to the mean concentration of nectar found in flowers pollinated by generalist avian nectarivores (reviewed by Johnson and Nicolson, 2008). The higher concentrations (15–25%) are similar to the mean concentration of nectar in flowers pollinated by specialist avian nectarivores (reviewed by Johnson and Nicolson, 2008).

Solutions were offered for 12 h (06:00–18:00 h) in a pairwise fashion from two 50 ml glass burettes placed 6 cm on either side of a central perch. The glass burettes were cut at the base and stopped with thick rubber rings that fitted tightly onto white plastic bird feeder bases. The fluids were thus presented to birds from identical cup-like structures with approximately 2 cm³ surface area each. Initial left and right positions were randomized for each bird and switched after 6 h. On dilute diets some burettes required refilling, done from the same original nectar solution. Control burettes of each solution were placed in the experimental room to account for evaporation.

Birds were weighed to the nearest 0.5 g before and after every trial. In order to account for inter-individual variation of body mass, volumes consumed were divided by the mass of each bird before analysis (ml g⁻¹). Preference for sucrose was calculated as a proportion: (ml g⁻¹ sucrose total ml g⁻¹ consumed) and then arcsine square-root transformed.

Apparent absorption efficiency

Apparent absorption efficiency of the two sugars was tested indirectly following a method similar to that used by Jackson et al. (Jackson et al., 1998b). Each sugar solution was tested at the 8.22% SE and 25% SE concentrations (*N* = 10). The weavers were housed individually in wire-mesh-floored cages (40 cm × 40 cm × 40 cm with mesh 2 cm × 1 cm × 1 cm), placed over a tray containing a layer of liquid paraffin ± 1.5 cm deep. Each sugar solution was available

to birds between 06:00–18:00 h using the same glass burettes above. Excreta were collected at 06:00 h the following morning.

Cloacal fluid was obtained from the liquid paraffin using a needled (1 ml) syringe and weighed to the nearest 0.01 g. Because cloacal fluid was extremely dilute (see below) with a density close to 1.0 and because direct measurements of cloacal fluid volume (to the nearest 0.01 ml) were statistically indistinguishable from estimates based on mass (paired-samples *t*-test: d.f.=9; *t*=-1.14; *P*=0.28), we used the latter. After thorough shaking, a 1.5 ml sub-sample from each bird was extracted and centrifuged at 6088 *g* for 3 min. Excreta was filtered with a 0.45 µm syringe filter and centrifuged again. 200 µl of the supernatant was analyzed for sugar concentrations using a high-performance liquid chromatograph (HPLC, Shimadzu, Duisburg, Germany). Detection was by refractive index (RID – 10 A) with a Phenomenex column (Rezex RCM-Monosaccharide, Aschaffenburg, Germany, 200 mm×780 mm×8 µm). Isocratic separation was accomplished using ultrapure water as the mobile phase.

Apparent absorption efficiency (AE) was calculated as (Jackson et al., 1998a):

$$AE = 100 \times [(sugar_{in}) - (sugar_{out}) / (sugar_{in})],$$

where (sugar_{in}) was a function of molar concentration and volume of nectar consumed; and (sugar_{out}) was a function of excreta volume and concentration of sugar in the excreta (mg ml⁻¹). Square-root transformed data was used to test the overall effects of sugar type and concentration on AE.

Transit times

Transit times were measured separately as the time taken from first ingestion of dyed nectar to the first appearance of dye in the excreta (Brown and Downs, 2003). Three ml of red food coloring (Robertsons, Cape Town, South Africa) was added to 500 ml of each of the same four nectar solutions. Birds were observed continuously until the appearance of dye in the excreta, at which time the trial was terminated. Eight birds were tested on each solution, on four different mornings, with maintenance diet being available for the remainder of the day.

Approval for this project was received from the Animal Ethics sub-committee of the University of KwaZulu-Natal. All birds were released at the capture site after the project was concluded.

RESULTS

Sugar preference

Village weavers showed significant preference for hexose sugars when offered solutions of 5% (one-sample *t*-test: *t*=2.408, *P*=0.039) and 10% (one-sample *t*-test: *t*=3.066, *P*=0.013) concentrations. They showed no significant preferences when offered solutions at concentrations of 15% (one-sample *t*-test: *t*=0.945, *P*=0.369), 20% (one-sample *t*-test: *t*=0.048, *P*=0.963) or 25% (one-sample *t*-test: *t*=0.165, *P*=0.873) (Fig. 1).

Total daily energy consumption (kJ g⁻¹ day⁻¹) was not significantly different between the five concentrations [repeated-measures analysis of variance (RMANOVA): *F*_{4,28}=1.378, *P*=0.267], as volumetric intake increased with decreasing concentration (Fig. 2). Birds did not lose body mass during any of the trials (RMANOVA: *F*_{4,36}=15.95, *P*=0.06).

Apparent absorption efficiencies

Apparent absorption efficiencies were affected by sugar type (RMANOVA: *F*_{1,9}=5.73, *P*=0.040), so that efficiency was greater for hexose nectars than for sucrose nectars (Table 1). Significant

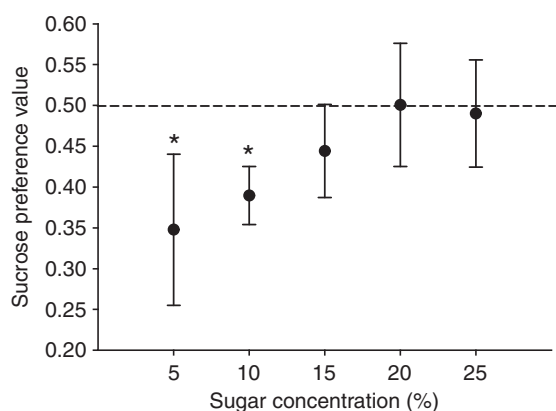


Fig. 1. Sugar preference of the village weaver *Ploceus cucullatus*, expressed as the proportion of ml g⁻¹ of sucrose nectar consumed in pairwise sucrose–hexose (1:1 fructose and glucose) choices (*N*=10). These were offered at five concentrations, measured in sucrose equivalents (SE). Bars indicate 95% c.i. * indicate significant preferences.

differences between hexose and sucrose sugars occurred at both low (paired-sample *t*-test: *t*=1.99, *P*=0.039) and high concentrations (paired-sample *t*-test: *t*=2.00, *P*=0.038). Despite lower absorption rates of sucrose, the birds maintained body mass during both 12 h sucrose diet trials [RMANOVA: *F*_{1,9}(time)=0.002, *P*=0.97].

Nectar concentration did not influence absorption efficiency (RMANOVA: *F*_{1,9}=3.87, *P*=0.081), so that both hexose absorption (paired-sample *t*-test: *t*=1.09, *P*=0.15) and sucrose absorption (paired-sample *t*-test: *t*=1.53, *P*=0.08) were independent of concentration.

Transit times

Nectar sugar composition had a significant effect on transit time (RMANOVA: *F*_{1,7}=12.39, *P*=0.010), with sucrose solutions passing through the digestive tract more quickly (Table 1). Paired-sample *t*-tests showed differences at low [*P* (1-tailed)=0.038] and high concentrations [*P* (1-tailed)=0.014].

Nectar concentration also affected transit times (RMANOVA: *F*_{1,7}=5.68, *P*=0.048), with lower concentrations passing through the digestive tract more quickly. Paired-sample *t*-tests revealed real differences between concentrations of sucrose [*P* (1-tailed)=0.034]

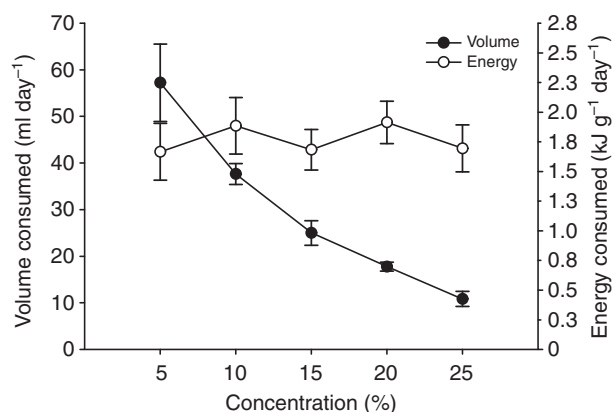


Fig. 2. Adjustment of volumetric intake (left axis) by village weaver *Ploceus cucullatus* resulting in similar energy intake (right axis) across five different concentrations (*N*=10). Values presented are means ± s.e.

Table 1. Effect of sugar type and concentration on both apparent absorption efficiency and retention time in village weavers (mean ± s.e.)

		Sugar concentration	
		8.22%	25%
Apparent absorption efficiency (%)	Sucrose	89.6±2.9	93.6±1.7
	Hexose	96.0±1.4	97.5±0.6
Transit time (s)	Sucrose	41.7±6.9	56.0±7.0
	Hexose	67.9±13.4	132.7±30.9

and hexose nectars [P (1-tailed)=0.040]. Transit times were independent of an intake response, as there was no overall relationship between volume consumed and transit time (least-squares regression: $R^2=0.04$, $P=0.28$). For each diet offered separately, this relationship was marginally significant only for the 25% SE hexose solution, with a low percentage of variance explained (regression: $R^2=0.55$, $P=0.035$).

DISCUSSION

The results of this study are consistent with our prediction that village weavers have a preference for hexose over sucrose sugar when offered solutions as dilute as those found in plants adapted for pollination by these birds (Fig. 1). A preference for hexose sugars is consistent with most of the previous studies on occasional nectarivores, except that tests on most of these species were conducted with high or intermediate concentration solutions, and most did not use equicaloric solutions (Martínez del Río et al., 1989; Malcarney et al., 1994; Franke et al., 1997; Lane, 1997). At high concentrations (20% and 25% SE) village weavers showed no sugar preference (Fig. 1). At 15% [which is at the lower end of the range for nectar concentration in specialist-pollinated flowers (Johnson and Nicolson, 2008), and at low concentrations of 5% and 10% [typical of plants pollinated by generalist avian nectarivores (Johnson and Nicolson, 2008)], village weavers preferred hexose nectar solutions (Fig. 1). This dependence of preference on concentration has been shown for specialist nectarivorous birds (Schondube and Martínez del Río, 2003; Fleming et al., 2004; Fleming et al., 2008; Brown et al., 2010a) but has not been demonstrated previously for a generalist avian nectarivore.

Importantly, birds were able to maintain body mass on low concentrations, and met daily energy requirements, similar to dark-capped bulbuls (Brown et al., 2010b). This contrasts with most specialist avian nectarivore species, which are unable to meet energy demands at very low concentrations (Nicolson and Fleming, 2003; Fleming et al., 2004; Fleming et al., 2008; Brown et al., 2010a). This could be a result of relatively slow transit times, allowing for better absorption at low concentrations.

Slow transit times do not, however, account for why village weavers did not maintain a hexose preference when offered high concentration nectars. In this case birds were probably able to extract sufficient resources from either solution, because of the readily available energy contained therein. This would reduce the limitation caused by possible non-optimal sucrase activity. In addition, sucrose preference at high concentrations in specialist nectarivores has been explained by osmotic pressure differences between the two sugars (Schondube and Martínez del Río, 2003). A high concentration of ingested hexose, consisting of many molecules, causes dehydration by osmotic water movement into the gut (Schondube and Martínez del Río, 2003). When no additional water is offered, as in this study, dehydration can be minimized by drinking sucrose solutions. When offered concentrated solutions, the lack of any particular preference by village weavers may indicate a balancing of the limitations of a sucrase deficiency and dehydration.

Physiological explanations for a hexose preference that have been suggested in the literature include sucrase deficiency (Brugger, 1992), sucrose hydrolysis rate limitations because of short retention times (Schondube and Martínez del Río, 2003) and/or superficial taste (Lotz and Schondube, 2006). At low concentrations any of these factors may be at work in village weavers.

Our results for sucrose absorption efficiency suggest that sucrose sugars were not hydrolyzed and assimilated as optimally as hexose sugars are assimilated (Table 1). This difference was significant at both concentrations, although more pronounced for dilute nectars. Although the method of analyzing sucrose absorption is not a direct assessment of sucrase activity, sugarbirds, sunbirds and white-eyes have been shown to assimilate both hexose and sucrose with nearly 100% efficiency using the same methodology, or with alternative refractometer-based sugar analysis methods that tend to underestimate efficiency (Downs, 1997b; Lotz and Nicolson, 1996; Jackson et al., 1998b; Franke et al., 1997). Compared with these species, village weavers do not effectively assimilate sucrose. However, unlike bird species that cannot assimilate sucrose at all (Muscicapoidea superfamily), and hence avoid sucrose solutions altogether (Gatica et al., 2006; Malcarney et al., 1994), village weavers consumed relatively large volumes of sucrose solutions. Furthermore, even though these birds appear to be less effective at extracting energy from sucrose nectars, sufficient absorption was achieved on sucrose-only diets to enable birds to maintain body mass over 12 h. This is consistent with the suggestion by Martínez del Río et al. (Martínez del Río et al., 1988) that birds that have primarily granivorous diets, containing complex carbohydrates, may have increased enzymatic activity, making them more tolerant of sucrose diets than insectivorous birds.

The second physiological explanation for hexose preference, sucrose hydrolysis rate limitation, is partly supported by transit times for village weavers. Faster transit times for sucrose, which were independent of volume intake (Table 1), may limit the time available for the breakdown of this sugar.

The reason why nectars produced by plants pollinated by generalist birds tend to have a low proportion of sucrose has not previously been satisfactorily explained (Johnson and Nicolson, 2008). It seems likely that differences in nectar properties between plants pollinated by specialist avian nectarivores and those pollinated by generalist ones are due to differences in selection imposed by these two groups of birds but this is still poorly understood (Fleming et al., 2004). The results reported here, along with those of Brown et al. (Brown et al., 2010b), reveal that sugar preferences and digestive abilities of occasional nectarivores like village weavers and dark-capped bulbuls, when offered solutions of biologically realistic concentrations, could explain the evolution of the hexose-dominated nectar in plants pollinated by these birds. Additional studies on generalized avian nectarivores would indicate whether this type of selective pressure is stable and widespread across a diversity of avian taxa.

An outstanding dilemma yet to be satisfactorily explained is the evolution of very dilute nectar in flowers pollinated by generalist

birds (Johnson and Nicolson, 2008). Non-specialist nectarivorous birds have a range of resources from which to access energy. Thus, the use of nectar in their diet may be dependent on the availability of other resources (Franklin and Noske, 1999). It has been hypothesized that preferences for concentrated nectar by these birds may become weak when such resources are not restricting or, alternatively, that nectars are used mainly as a water resource in the dry months (Oatley and Skead, 1972; Johnson and Nicolson, 2008; Symes et al., 2008). Although the sugar preferences and digestive capacities presented here suggest pollinator-mediated selection for hexose sugars when nectar is dilute, experiments that untangle the relative importance of nectar for energy and water balance would contribute further to understanding the nectar properties of flowers pollinated by generalist birds.

ACKNOWLEDGEMENTS

Thamsanqa Mjwara is thanked for housing and helping to care for the birds. A. A. Odendaal for indispensable deliberations, assistance and comments. Nkubekheze Dlamini and Charlotte Goulon are thanked for assistance in data collection.

REFERENCES

- Baker, H. G. and Baker, I. (1983). Floral nectar sugar constituents in relation to pollinator type. *Handbook of Experimental Pollination Biology* (ed. C. E. Jones and R. J. Little), pp. 117-141. New York: Scientific and Academic Press.
- Botes, C., Johnson, S. D. and Cowling, R. M. (2008). Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology. *Oikos* **117**, 875-882.
- Brown, K. J. and Downs, C. T. (2003). Digestive efficiency of a generalist avian feeder, the Cape White-eye (*Zosterops pallidus*). *Comp. Biochem. Physiol. A* **134**, 739-748.
- Brown, M., Downs, C. T. and Johnson, S. D. (2008). Sugar preferences of nectar feeding birds – a comparison of techniques. *J. Avian Biol.* **39**, 479-483.
- Brown, M., Downs, C. T. and Johnson, S. D. (2009). Pollination of the red-hot poker *Kniphofia caulescens* by short-billed opportunistic avian nectarivores. *S. Afr. J. Bot.* **75**, 707-712.
- Brown, M., Downs, C. T. and Johnson, S. D. (2010a). Concentration-dependent sugar preferences of the Malachite Sunbird *Nectarinia famosa*. *Auk* **127**, 151-155.
- Brown, M., Downs, C. T. and Johnson, S. D. (2010b). Sugar preferences and digestive efficiency in an opportunistic avian nectarivore, the Dark-capped Bulbul *Pycnonotus tricolor*. *J. Ornithol.* Epub. doi:10.1007/s10336-010-0498-8
- Brugger, K. E. (1992). Repellency of sucrose to captive American Robins. *J. Wildl. Manage.* **56**, 794-799.
- Brugger, K. E. and Nelms, C. O. (1991). Sucrose avoidance by American robins (*Turdus migratorius*): Implications for control of bird damage in fruit crops. *Crop Prot.* **10**, 455-460.
- Brugger, K. E., Nol, P. and Phillips, C. I. (1993). Sucrose repellency to European starlings: will high-sucrose cultivars deter bird damage to fruit? *Ecol. Appl.* **3**, 256-261.
- Cruden, R. W. and Toledo, V. M. (1977). Oriole pollination of *Erythrina breviflora* (Leguminosae): evidence for a polytypic view of ornithophily. *Plant Syst. Evol.* **126**, 393-403.
- Daniels, C. L. (1987). *The feeding ecology of nectarivorous birds in the Natal Drakensberg*. Masters of Science MSc Thesis, University of Natal, Pietermaritzburg.
- Downs, C. T. (1997a). Sugar preference and apparent sugar assimilation efficiency in the Red Lory. *Aust. J. Zool.* **45**, 613-619.
- Downs, C. T. (1997b). Sugar digestion efficiencies of Gurney's Sugarbirds, Malachite Sunbirds and Black Sunbirds. *Physiol. Zool.* **70**, 93-99.
- Downs, C. T. and Perrin, M. R. (1996). Sugar preferences of some southern African nectarivorous birds. *Ibis* **138**, 455-459.
- Dupont, Y. L., Hansen, D. M., Rasmussen, J. T. and Olesen, J. M. (2004). Evolutionary changes in nectar sugar composition associated with switches between bird and insect pollination: the Canarian bird-flower element revisited. *Funct. Ecol.* **18**, 620-676.
- Fleming, P. A., Hartman Bakken, B., Lotz, C. N. and Nicolson, S. W. (2004). Concentration and temperature effects on sugar intake and preferences in a sunbird and a hummingbird. *Funct. Ecol.* **18**, 223-232.
- Fleming, P. A., Xie, S., Napier, K., McWhorter, T. J. and Nicolson, S. W. (2008). Nectar concentration affects sugar preferences in two Australian honeyeaters and a lorikeet. *Funct. Ecol.* **22**, 599-605.
- Franke, E., Jackson, S. and Nicolson, S. W. (1997). Nectar sugar preferences and absorption in a generalist African frugivore, the Cape White-eye *Zosterops pallidus*. *Ibis* **140**, 501-506.
- Franklin, D. C. and Noske, R. A. (1999). Birds and nectar in a monsoonal woodland: correlations at three spatio-temporal scales. *Emu* **99**, 15-28.
- Gatica, C. D. L., González, S. P., Vásquez, R. A. and Sabat, P. (2006). On the relationship between sugar digestion and diet preference in two Chilean avian species belonging to the Muscicapidae superfamily. *Revista Chilena de Historia Natural* **79**, 287-294.
- Hainsworth, F. R. and Wolf, L. L. (1976). Nectar characteristics and food selection by hummingbirds. *Oecologia* **25**, 101-113.
- Jackson, S., Nicolson, S. W. and Lotz, C. N. (1998a). Sugar preferences and 'side bias' in Cape Sugarbirds and Lesser Double-collared Sunbirds. *Auk* **115**, 156-165.
- Jackson, S., Nicolson, S. W. and Van Wyk, B. E. (1998b). Apparent absorption efficiencies of nectar sugars in the Cape Sugarbird, with a comparison of methods. *Physiol. Zool.* **71**, 106-115.
- Johnson, S. D. and Nicolson, S. W. (2008). Evolutionary associations between nectar properties and specificity in bird pollination systems. *Biol. Lett.* **4**, 49-52.
- Johnson, S. D., Hargreaves, A. L. and Brown, M. (2006). Dark, bitter-tasting nectar functions as a filter of flower visitors in a bird-pollinated plant. *Ecology* **87**, 2709-2716.
- Lane, S. J. (1997). Preferences and apparent digestibilities of sugars by fruit damaging birds in Japan. *Ann. Appl. Biol.* **130**, 361-370.
- Lotz, C. N. and Nicolson, S. W. (1996). Sugar preferences of a nectarivorous passerine bird, the Lesser Double-collared Sunbird (*Nectarinia chalybea*). *Funct. Ecol.* **10**, 360-365.
- Lotz, C. N. and Schondube, J. E. (2006). Sugar preferences in nectar- and fruit-eating birds: behavioral patterns and physiological causes. *Biotropica* **38**, 3-15.
- Malcarney, H. L., Martínez del Río, C. and Apanius, V. (1994). Sucrose intolerance in birds: simple non-lethal diagnostic methods and consequences for assimilation of complex carbohydrates. *Auk* **111**, 170-177.
- Martínez del Río, C. (1990). Sugar preferences in hummingbirds: the influence of subtle chemical differences on food choice. *Condor* **92**, 1022-1030.
- Martínez del Río, C. and Stevens, B. R. (1989). Physiological constraints on feeding behavior: intestinal membrane disaccharidases of the Starling. *Science* **243**, 794-796.
- Martínez del Río, C., Stevens, B. R., Daneke, D. E. and Andreadis, P. T. (1988). Physiological correlates of preference and aversion for sugars in three species of birds. *Physiol. Zool.* **61**, 222-229.
- Martínez del Río, C., Karasov, W. H. and Levey, D. J. (1989). Physiological basis and ecological consequences of sugar preferences in Cedar Waxwings. *Auk* **106**, 64-71.
- Martínez del Río, C., Baker, H. G. and Baker, I. (1992). Ecological and evolutionary implications of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. *Experientia* **48**, 544-551.
- Martínez del Río, C., Schondube, J. E., McWhorter, T. J. and Herrera, L. G. (2001). Intake responses in nectar feeding birds: digestive and metabolic causes, osmoregulatory consequences, and coevolutionary effects. *Am. Zool.* **41**, 902-915.
- Mata, A. and Bosque, C. (2004). Sugar preferences, absorption efficiency and water influx in a Neotropical nectarivorous passerine, the Bananaquit (*Coereba flaveola*). *Comp. Biochem. Physiol. A* **139**, 394-404.
- Nicolson, S. W. and Fleming, P. A. (2003). Nectar as food for birds: the physiological consequences of drinking dilute sugar solutions. *Plant Syst. Evol.* **238**, 139-153.
- Oatley, T. B. (1964). The probing of Aloe flowers by birds. *Lammergeyer* **3**, 2-8.
- Oatley, T. B. and Skead, D. M. (1972). Nectar feeding by South African birds. *Lammergeyer* **15**, 65-74.
- Roberts, W. M. (1996). Hummingbirds' nectar concentration preferences at low volume: the importance of time scale. *Anim. Behav.* **52**, 361-370.
- Schondube, J. E. and Martínez del Río, C. (2003). Concentration-dependent sugar preferences in nectar-feeding birds: mechanisms and consequences. *Funct. Ecol.* **17**, 445-453.
- Schuler, W. (1983). Responses to sugars and their behavioural mechanisms in the starling (*Sturnis vulgaris* L.). *Behav. Ecol. Sociobiol.* **13**, 243-251.
- Stiles, F. G. (1976). Taste preferences, color preferences, and flower choice in hummingbirds. *Condor* **78**, 10-26.
- Symes, C. T., Nicolson, S. W. and McKechnie, A. E. (2008). Response of avian nectarivores to the flowering of *Aloe marlothii*: a nectar oasis during dry South African winters. *J. Ornithol.* **149**, 13-22.
- Symes, C. T., Human, H. and Nicolson, S. W. (2009). Appearances can be deceiving: pollination in two sympatric winter-flowering Aloe species. *S. Afr. J. Bot.* **75**, 668-674.
- Wykes, G. R. (1952). The preferences of honeybees for solutions of various sugars which occur in nectar. *J. Exp. Biol.* **29**, 511-519.