

SUGAR PREFERENCES AND "SIDE BIAS" IN CAPE SUGARBIRDS AND LESSER DOUBLE-COLLARED SUNBIRDS

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ABSTRACT.—Using pairwise feeder tests, we studied preferences for sugars in Cape Sugarbirds (*Promerops cafer*) and Lesser Double-collared Sunbirds (*Nectarinia chalybea*). Birds were offered 20% (w:w) solutions of sucrose, fructose, glucose, and a mixture of equal parts of glucose and fructose. Cape Sugarbirds showed no preference among these sugars, whereas the order of preference in Lesser Double-collared Sunbirds was sucrose > fructose = hexose mixture > glucose. Both species showed strong "side biases," with individuals consistently drinking more from feeders offered on a particular side of the feeder pair. We suggest that this bias is a manifestation of stereotyped foraging behavior rather than lateralization or true "handedness." The absence of a sucrose aversion in "fynbos" (i.e. Cape Floristic Kingdom of southern Africa) nectarivores such as sugarbirds and sunbirds is not surprising because the fynbos is characterized by high floral diversity and low bird diversity and by the occurrence of both sucrose-dominant and hexose-dominant nectars. However, our findings contradict an earlier generalization that passerines prefer hexoses to sucrose. This generalization is based on studies of several American and European species and of one East African species, and it may be confounded by comparisons of specialized nectarivorous non-passerines with generalized frugivorous/nectarivorous passerines. In separate feeding trials, both sugarbirds and sunbirds showed a strong aversion to the pentose sugar xylose, a nectar sugar newly described for the Proteaceae. The reason for the occurrence of xylose in nectar of the Proteaceae is unknown. Received 19 August 1996, accepted 1 July 1997.

TASTE PREFERENCES of avian nectarivores are related to nectar composition of their food plants (Martínez del Río 1990, Martínez del Río et al. 1992) and to the birds' phylogenetic lineages (Martínez del Río and Stevens 1989). Most of the literature on this subject has focused on New World species such as hummingbirds and members of the passerine sturnid-muscicapid lineage (e.g. Hainsworth and Wolf 1976, Stiles 1976, Tamm and Gass 1986, Martínez del Río et al. 1992), revealing sucrose intolerance and aversion among the passerines but not among hummingbirds. Recent studies have reported sucrose-dominant nectars in many ornithophilous *Erica* species in the Cape fynbos of South Africa (Barnes et al. 1995) and have revealed a new nectar sugar, xylose, in *Protea* and *Faurea* (van Wyk and Nicolson 1995). Because their food plants have different nectar sugars from those found in America, and because they represent a new taxonomic group for which sugar-type preferences have been little studied (but see Lotz and Nicolson 1996),

we investigated sugar preferences in two fynbos nectarivores, the Cape Sugarbird (*Promerops cafer*) and the Lesser Double-collared Sunbird (*Nectarinia chalybea*). The Cape Sugarbird is one of the two species comprising the family Promeropidae and is endemic to the southwestern Cape region of South Africa. Its closest relatives are the sunbirds (Nectariniidae). We refer to our study species as "sugarbirds" and "sunbirds," respectively.

Taste-preference experiments in caged nectarivorous birds involve offering a choice of two or more solutions to the birds and measuring the relative volumes consumed. Using pairwise comparisons, previous authors have offered two different solutions in two feeders (Rogers and Maller 1973; Hainsworth and Wolf 1976; Schuler 1983; Lloyd 1989; Martínez del Río et al. 1988, 1989; Martínez del Río 1990; Brugger 1992; Lotz and Nicolson 1996), or alternating in four feeders in a row (Tamm and Gass 1986) or in a ring (Bartholomew and Cade 1958). Others have offered different solutions one at a time on separate days (Clarke et al. 1991), or have offered three different solutions simultaneously (Stiles 1976). Researchers have controlled for potential positional biases by

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switching feeder positions periodically during each feeding trial (Hainsworth and Wolf 1976) or between feeding trials on separate days (Tamm and Gass 1986), or by randomly assigning solutions to different feeders (Stiles 1976, Schuler 1983, Martínez del Rio et al. 1988, Lotz and Nicolson 1996). Roberts (1996) offered hummingbirds a choice between paired sugar solutions of different concentrations over two consecutive days, reversing the positions of the solutions on the two days. Possible ways of presenting food to hummingbirds have been reviewed by Gass (1978).

In the presence of strong positional biases or "handedness" in birds, randomly assigning and/or switching feeder positions may mask taste preferences without adequately separating the effects of position, particularly if the taste preferences are not strong. In half of their tests for sugar preferences in hummingbirds, and in all their tests for amino acid preferences, Hainsworth and Wolf (1976) found that positional preferences overrode taste. Handedness has been researched intensively in humans and nonhuman primates (see MacNeilage et al. 1987), and its presence in songbirds has been established (Denenberg 1981). Gass (1978) is one of the few authors studying taste preferences in nectarivores who has discussed the issue. In our study of sunbirds and sugarbirds, we addressed this issue in greater depth and strived to separate the effects of feeder position from those of taste. Our results for Lesser Double-collared Sunbirds supplement data on sugar preferences that were collected using an experimental protocol very similar to that of the present study but which did not take "side biases" into account (Lotz and Nicolson 1996). We now rectify this shortcoming.

METHODS

Bird capture and maintenance.—Adult birds were caught during the nonbreeding season (March to April 1995 and October 1995) using mist nets, and were housed separately in cages measuring 70 × 80 × 40 cm (sugarbirds) and 52 × 52 × 52 cm (sunbirds). The cages were covered with plastic-coated screen mesh (sugarbirds) or 30% shade cloth (sunbirds). We used 13 Lesser Double-collared Sunbirds (seven males and six females) and 13 Cape Sugarbirds. Only female sugarbirds were used, because the long tails of males hamper their movements in cages, and there is no *a priori* evidence supporting a sex-linked difference in diet or sugar preferences.

Birds were acclimated to captivity for four to six weeks, depending on date of capture, in outdoor enclosures sheltered from rain and wind. For the feeding trials, birds were moved to a laboratory where their cages were placed next to windows to approximate natural light cycles as closely as possible. Here, ambient temperature was partly controlled and ranged from 18 to 24°C. Sugarbirds had access at all times to fresh bathing and drinking water in dishes that were removed only during feeding trials. Sunbirds did not bathe daily as did the sugarbirds, and therefore were not offered bathing water as frequently.

Birds were fed a mixture of 4.2 g each of sucrose, glucose, and fructose, plus 2.5 g of Complian (Boots Pharmaceuticals, Isando, South Africa), per 100 mL of water. The sugar concentration of this solution is thus 10.95%. This diet is adequate for maintenance of body mass and health in Australian honeyeaters and in Lesser Double-collared Sunbirds (Collins and Morellini 1979, Lotz and Nicolson 1996). Throughout this study, we used solutions made up on the basis of solute mass, rather than molarity, and all references to relative solute masses and solution concentrations (%) are on a weight:weight basis (i.e. weight solute:weight solution).

The solution was presented to the birds *ad libitum* in plastic feeders that are commercially manufactured for feeding graminivorous caged birds. These feeders have a colored plastic base with a protruding trough 3 cm long and 0.8 cm wide and a vertical well made of clear plastic that holds up to 120 mL of solution. Food was changed twice daily. At the end of the experiments, the birds were banded and released at the site of capture.

Preference tests.—During preference tests we used glass feeders made from 25-mL pipettes that permit measurement of volumes consumed to the nearest 0.05 mL. The bottom end of the pipette was expanded to form a glass bulb 2.5 cm in diameter, with a circular hole 4 to 5 mm in diameter. The drinking aperture was surrounded by a ring of red nail varnish (3 mm wide) to enhance its visibility; paired feeders were offered to the birds with the apertures 3 cm apart. Birds could thus reach both feeders in one visit, and choice between feeders did not involve an energetic element. Before the start of experiments, we checked that no spillage occurred from feeders by resting the feeder bulbs on white paper sheets and checking the sheets for signs of wetting. No such signs were observed after 4 to 8 h for any of the feeders used.

Feeder placement and side biases.—During initial habituation to glass feeders, both sugarbirds and sunbirds were offered two feeders containing the same solution, a 15 or 20% aqueous solution containing equal weights of sucrose, glucose, and fructose. Volumes of solution consumed from each feeder were calculated as the difference between final and initial

TABLE 1. Preference indices ($[\text{volume of left sugar consumed} / \text{total volume consumed}] \times 100$) for 20% sugar solutions offered in pairs to Cape Sugarbirds. Column headings are sugar pairs, with left sugar first. S, sucrose; F, fructose; G, glucose; M, mixture of equal masses of glucose and fructose; ND, no data. Instances where birds switched their side preferences from one day to the next in response to change in sugar type are in bold italics. Asterisks denote a significant ($P < 0.05$) change in side bias.

Bird no.	Trial	SF	FS	SG	GS	SM	MS	FG*	GF*	FM	MF	GM	MG	\bar{x}
4	1	63	38	66	92	9	16	96	92	100	71	54	70	64
	2	93	96	100	100	48	92	94	99	98	100	96	100	93
6	1	100	100	100	100	100	100	100	100	100	100	98	100	100
	2	50	90	33	16	10	11	62	16	24	35	16	13	31
7	1	55	40	0	0	0	2	81	100	9	0	1	0	24
	2	100	ND	50	40	ND	33	100	100	50	75	50	ND	66
8	1	11	3	0	3	3	2	1	10	3	1	2	3	3
	2	0	1	20	16	2	1	9	1	8	7	2	1	6
9	1	1	0	0	0	1	1	1	0	0	0	1	3	1
	2	1	1	1	1	2	1	0	0	1	1	1	1	1
11	1	0	2	29	18	0	0	35	100	88	58	38	5	31
	2	0	0	100	85	60	77	100	48	93	87	88	52	66
12	1	0	17	29	36	8	1	43	78	1	0	0	2	18
	2	1	34	3	23	42	4	43	6	20	11	50	18	25
13	1	14	25	3	51	3	1	50	68	0	3	30	25	23
	2	2	3	2	1	2	0	29	1	12	3	0	1	5
14	1	2	8	25	0	41	14	0	20	6	9	17	7	12
	2	27	55	5	38	10	1	4	16	65	59	4	3	24
15	1	86	67	86	0	96	36	91	87	68	73	41	79	67
	2	88	43	91	16	96	29	56	48	29	51	29	0	48
16	1	73	18	41	99	30	5	ND	ND	53	44	71	49	48
	2	22	4	4	4	62	8	49	11	4	12	8	10	16
17	1	1	2	3	39	2	3	4	2	18	26	21	20	12
	2	17	1	1	1	2	0	1	32	5	17	2	3	7
18	1	52	84	36	62	94	93	71	62	68	79	80	84	72
	2	1	2	64	84	1	0	93	41	64	85	11	2	37

readings. All feeding trials started between 0900 and 0945 and lasted 4 h for sugarbirds and 6 h for sunbirds. After two days, it became obvious that individual birds preferred one or the other side, sometimes exclusively, but that neither species showed true "handedness," or bias for a particular side. We ascertained this using a two-tailed *t*-test to examine departures of preference indices (volume consumed from left feeder/total volume consumed) from a hypothetical mean of 0.5. We combined data from experiments 1 and 7 (described below), and from the two data sets summarized in Tables 1 and 2, using a single mean preference index for each individual bird. Preference indices were arcsine-transformed. There were no significant departures of overall preference indices from 0.5.

We then carried out a series of seven feeding trials in which we explored the effects of side biases on tests for sugar-type preference: (1) Paired feeders side by side with apertures 3 cm apart, placement in cage constant ($n = 9$ and 12 for sugarbirds and sunbirds, respectively, offered for two days); (2) a single feeder at each end of the cage (five birds, four days); (3) paired feeders with U-shaped ends (Martínez del Rio 1990) rather than bulbs, hence with the drinking

apertures 2 mm rather than 3 cm apart (five birds, three days); (4) four feeders in a row (five birds, two days); (5) four feeders in a row, with positions changed every hour by moving the feeder from the farthest right position in the row to the farthest left, so that each feeder occupied every position for 1 h (five birds, three days); (6) six feeders in a ring (three birds, one day); and (7) paired feeders switched on subsequent days from one end of the cage to the other (seven birds, four days). Sugarbirds and sunbirds were used in experiment 1, but only sugarbirds were used in experiments 2 to 7. On the basis of feeding patterns observed with these arrangements, we chose a simple pairwise presentation of adjacent feeders for the preference tests described below.

Sugar preferences.—We used the above protocol for sugarbirds and sunbirds to measure consumption of four 20% sugar solutions: pure glucose, pure fructose, pure sucrose, and an equal mixture of glucose and fructose (i.e. the hexose mixture). These offered a total of six possible pairwise combinations, the presentation order of which was randomized. Solutions were presented to the birds in two separate feeders that remained in one position throughout each feeding trial. The same sugar pair was presented on two

TABLE 2. Preference indices ([volume of left sugar consumed / total volume consumed] × 100) for 20% sugar solutions offered in pairs to Lesser Double-collared Sunbirds. Column headings are sugar pairs, with left sugar first. S, sucrose; F, fructose; G, glucose; M, mixture of equal masses of glucose and fructose. Instances where birds switched their side preferences from one day to the next in response to change in sugar type are in bold italics. Asterisks denote a significant (*, *P* < 0.05; **, *P* < 0.02) change in side bias.

Bird no.	Trial	SF	FS	SG**	GS**	SM**	MS**	FG	GF	FM	MF	GM*	MG*	\bar{x}
1	1	11	21	100	8	83	74	100	0	93	20	99	59	56
	2	10	2	97	10	64	52	89	1	48	25	1	56	38
2	1	96	98	100	99	100	100	97	100	98	99	97	100	99
	2	93	91	100	100	97	100	98	100	100	100	98	100	98
3	1	4	4	0	1	2	1	0	0	11	12	31	7	6
	2	99	99	94	100	94	93	100	99	99	99	99	99	98
4	1	88	73	91	12	33	0	99	6	97	72	12	85	56
	2	23	55	95	7	91	0	71	17	100	7	31	78	48
5	1	91	39	89	11	100	10	100	39	100	98	100	67	70
	2	100	93	100	100	100	100	100	69	98	94	96	99	96
6	1	100	98	97	97	98	100	100	100	100	95	100	99	99
	2	4	0	0	0	0	0	9	1	0	2	7	100	10
7	1	0	35	42	0	32	8	2	17	23	48	47	0	21
	2	46	41	2	0	4	0	0	26	0	69	7	0	16
8	1	61	78	17	10	76	0	16	5	37	9	10	23	28
	2	0	0	4	0	97	29	3	1	0	0	0	0	11
9	1	88	1	37	2	8	5	31	57	35	7	21	50	29
	2	78	70	93	87	90	6	85	9	39	22	36	45	55
10	1	97	50	96	23	99	9	97	7	91	99	50	97	68
	2	43	37	99	0	98	6	92	16	39	87	3	97	51
11	1	0	1	3	3	4	2	2	2	0	0	0	0	1
	2	0	2	1	2	0	2	0	1	1	0	2	1	1
12	1	1	0	3	8	2	5	2	6	0	0	0	19	4
	2	2	0	2	6	2	0	1	4	0	0	1	0	2
13	1	94	14	73	3	93	37	88	42	93	10	22	93	55
	2	61	2	97	1	69	4	61	45	96	7	6	96	45

consecutive days, with the position of the solutions reversed on the second day and with the order of initial presentation randomized. Each series of trials therefore lasted 12 days, and we carried out two complete series for each species. Sugar solutions were made up using reagent grade D-glucose, D-fructose, sucrose (Saarchem, Cape Town), and distilled water.

For each sugar pair presented, we performed a separate paired-sample Wilcoxon test on ranked preference indices (volume of left-hand sugar consumed / total volume consumed) for the consecutive days on which sugar positions were reversed. In all cases, two series of trials were carried out. A significant difference between the two days suggests that a bird changed its side preference in response to changes in the sugar types offered in the two feeders on successive days.

A fifth 20% solution of pure xylose (analytical grade; Saarchem, Cape Town) was included in an initial series of feeding trials on sugarbirds that was abandoned after two days. During those two days, a randomly selected subset of five birds was scheduled to receive xylose in combination with one of the other sugar solutions. Of these five birds, two showed signs of disorientation and weakness after drinking

5.7 and 4.9 mL of the xylose solution over 2 h, one drank 6 mL of xylose with no apparent ill effects, and two drank greatly reduced volumes of xylose when this was presented on their favored side (2.1 mL and 1.2 mL vs. 13.9 mL and 9.7 mL, respectively, of the palatable mixture presented on the same side on the previous day). This feeding-trial series was terminated, and its results taken as sufficient evidence of a xylose aversion to warrant a separate treatment of xylose taste preferences. Lesser Double-collared Sunbirds are averse to pure 20% xylose and to a 30% mixture comprising 20% glucose and 10% xylose (Lotz and Nicolson 1996).

To explore the effects of xylose concentration on taste preferences, we carried out a separate series of 4-h pairwise feeding trials on six sugarbirds. We offered the birds a choice between a 20% solution containing equal amounts of sucrose, glucose, and fructose, and a 20% solution of which xylose constituted 10 to 100% of the total sugar and equal parts of glucose, fructose, and sucrose the remaining sugar moiety. Xylose concentrations in the nectar of *Faurea* and *Protea* spp. range from 0 to 39% of total nectar sugar (van Wyk and Nicolson 1995). Feeders containing xylose were placed on each bird's favored side (established from the preceding series of trials). Only

TABLE 3. Results of nonparametric two-factor ANOVAs testing for effect of feeder arrangements on side biases in Cape Sugarbirds (all experiments) and Lesser Double-collared Sunbirds (experiment 1 only).

Experiment	H	df	P
(1) Paired feeders, positions constant (sugarbirds)	25.9	1	<0.001
(1) Paired feeders, positions constant (sunbirds)	24.2	1	<0.001
(2) Single feeder at each end of cage	29.3	1	<0.001
(3) Paired U-shaped feeders	5.1	1	<0.025
(4) Four adjacent feeders in a row	32.4	3	<0.001
(5) Four feeders in a row, positions rotated hourly	2.2	3	>0.50
(6) Six feeders in a ring ^a	—	—	—
(7) Paired feeders switched daily from one end of cage to another	21.3	6	<0.005

^a Sample sizes too small for testing.

birds with consistent side preferences were used. We progressively increased the size of the xylose moiety of the 20% total sugar in solution so that xylose constituted 10, 20, 30, 40, 50, 60, 80, and 100% of total sugar on successive days.

RESULTS

Feeder placement and side biases.—When presented with the same solution in feeders arranged in various ways, both sugarbirds and sunbirds showed strong and consistent side biases that overrode variation among individuals in volume consumed. Individual birds consistently drank more from one feeder when feeders were presented as a pair, but neither species showed true “handedness,” i.e. an overall bias for a particular side (Tables 1 and 2).

On the strength of the finding that individual side biases were consistent but randomly distributed among individuals, we categorized feeder positions into favored (side from which more than 50% of the total volume for the first day of each trial was consumed) and nonfavored, and tested for changes in side preferences within individual birds when feeder arrangements were altered. All feeders contained the same solution (20% equal mixture of all three sugars). We used nonparametric two-factor ANOVAs (Zar 1984) on volumes consumed to assess the significance of two main effects: feeder position and differences among individuals (see Table 3). In all cases the interaction between the main effects was not statistically significant, and individual variation had no effect on volume consumed except for experiment 7. To illustrate the persistence of side biases in both bird species, we show data for experiment 1 (see Figs. 1 and 2), but for brevity we have not included data for every experiment. Total volumes consumed by individual birds did not differ among the different feeding trials.

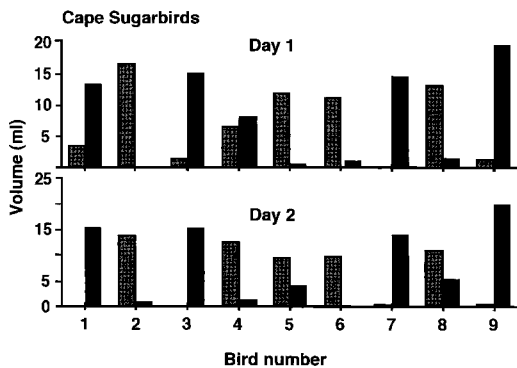


FIG. 1. Volumes of a 20% aqueous solution of equal parts sucrose, fructose, and glucose consumed by nine Cape Sugarbirds from left (shaded bars) and right (solid bars) feeders presented in pairs on two consecutive days. Differences between left and right sides were consistent and significant within individuals (Kruskal-Wallis two-factor ANOVA), and the mean overall preference index did not differ significantly from 0.5.

Xylose aversion.—Six sugarbirds presented with a 20% solution of fructose/sucrose/glucose mixed with increasing concentrations of xylose consumed significantly less of the solution as the xylose fraction approached 100% of total sugar content over nine successive days (Kruskal-Wallis single-factor ANOVA, $H = 36.46$, $df = 8$, $P < 0.001$; Fig. 3). By the end of the trial, three of the six birds had switched their preference from the initially favored side to the side on which no xylose was presented.

Sugar preferences.—Sugar preferences for sugarbirds and sunbirds are reported in Tables 1 and 2, respectively. In view of the data presented above, side biases were considered a primary determinant of the volumes consumed

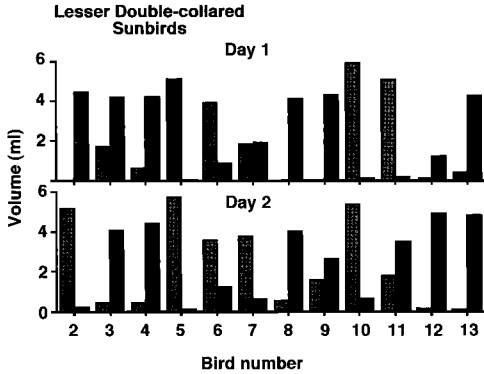


FIG. 2. Volumes of a 20% aqueous solution of equal parts sucrose, fructose, and glucose consumed by 12 Lesser Double-collared Sunbirds from left (shaded bars) and right (solid bars) feeders presented in pairs on two consecutive days. Differences between left and right sides were consistent and significant within individuals (Kruskal-Wallis two-factor ANOVA), and the mean overall preference index did not differ significantly from 0.5.

from different feeders. For each individual bird, we assumed that side biases were consistent for the two days on which each sugar pair was offered, and the experiments tested for departures from this habitual condition. Birds were presented with a given sugar pair on one day, and the same pair with the positions (left/right) of each sugar reversed on the following day, and the order of presentation of sugar types was randomized. Sugar-type preferences would be manifested by individual birds switching from their favored side to "follow" a particular sugar, with preference indices changing from less than 0.5 on one day to greater than 0.5 on the other, or vice versa. When switching occurred it was almost always pronounced (Tables 1 and 2), with nine individuals of each species showing switching on one or more occasion across all sugar combinations tested. For all instances when switching occurred, differences between preference indices on consecutive days were $0.40 \pm \text{SE}$ of 0.04 and 0.76 ± 0.03 for sugarbirds and sunbirds, respectively.

Sugarbirds (Table 1) demonstrated a significant preference for fructose over glucose in the second series of trials ($t = 17, n = 13, P < 0.05$), although no individual showed the same preference across both trials. Thus, an individual bird's bias usually overrode any preference for a particular sugar. One sugarbird (no. 6) shift-

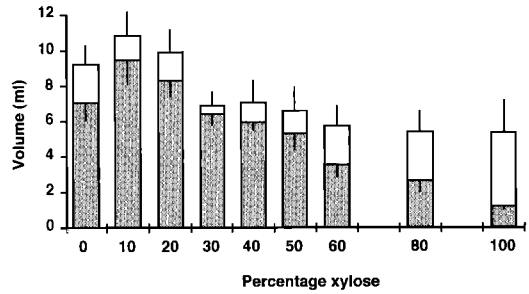


FIG. 3. Total volume of solutions consumed by six Cape Sugarbirds presented with a xylose solution and a sucrose/glucose/fructose solution over nine consecutive days. Increasing percentages of xylose were offered in a solution totaling 20% sugar (w:w). The remaining sugar component of the xylose solution comprised equal parts of sucrose, glucose, and fructose. The xylose solution was presented on each bird's favored side, paired with a 20% solution of sucrose, fructose, and glucose on the less-favored side. Shaded bars represent the mean volume of xylose solution ($\pm \text{SE}$) consumed from the birds' favored side on that day (at 0% xylose, shaded bar is the mean volume of solution consumed on the birds' favored sides). Entire bars (shaded plus clear sections) represent the mean total volume of both sugar solutions consumed, $\pm 1 \text{ SE}$.

ed from a left-hand bias in trial 1 to a right-hand bias in trial 2. In contrast, sunbirds (Table 2) showed significant preferences for sucrose over glucose (trial 1: $t = 3, P < 0.005$; trial 2: $t = 11, P < 0.02$) and for sucrose over the hexose mixture (trial 1: $t = 5, P < 0.005$; trial 2: $t = 11, P < 0.02$). Sunbirds also showed weak (bordering on significant) preferences for fructose over glucose ($t = 19$ and 18 for trials 1 and 2 respectively, $0.05 < P < 0.1$) and for the hexose mixture over glucose (trial 2: $t = 16, P < 0.05, n = 13$ in all cases). The above comparisons were within trials; only a minority of sunbirds showed the same preference in both trials (four preferred sucrose to glucose, and three preferred sucrose to the mixture). Thus, the order of sugar preference for sunbirds was sucrose > hexose mixture = fructose > glucose.

DISCUSSION

Feeder placement.—Side preferences in sugarbirds and sunbirds had a profound effect on their choice of a feeder. Both species showed distinct side preferences that almost always were consistent between consecutive days and

between replicate trials. Moreover, these preferences arose spontaneously while the birds were being fed identical solutions in paired feeders during the pre-experimental period of habituation to paired feeders (see Methods). Hourly switching of the four feeders in a row during the course of a feeding trial resulted in equal volumes being consumed from each feeder, presumably as it rotated through the favored position. However, this approach does not distinguish between the effects of position and of sugar preference on volumes consumed by the birds. Moreover, if feeders are rotated at intervals shorter than the length of time that birds take to associate a feeder position with a particular sugar, taste preferences may be obscured. This period may differ between hummingbirds and passerines, which employ different foraging strategies and which therefore may differ in the flexibility of their learning abilities. Consequently, we were reluctant to adopt the approach of Hainsworth and Wolf (1976), who switched feeders every 30 min and concluded that positional biases were as strong as sugar tastes in hummingbirds. Instead, we suggest that separation of the effects of position and food attributes (e.g. sugar type and concentration) be accomplished by adjusting the design of *ad libitum* feeding experiments (e.g. Roberts 1996, this study) and by randomizing the order of presentation of sugar-type pairs. *A priori* establishment of the presence or absence of side biases should be a routine precursor in preference experiments.

We were surprised to find that position was a more important determinant of volume consumed by Cape Sugarbirds than was sugar type, because we expected these nectarivores to have well-developed spatial memories and quick recognition of food attributes. Preference experiments assume that experimental subjects are able to discriminate between the solutions offered, and the simplified cues offered to our experimental birds may have been inadequate for discrimination. Birds in the field probably use a combination of color, taste, and spatial cues when foraging. For example, Schuler (1983) found that color association improved the ability of European Starlings (*Sturnus vulgaris*) to discriminate between sugar solutions. However, the fact that positional preferences occurred consistently between trials separated by several weeks suggests that birds retained

spatial memory of feeder positions that presumably also would have been adequate for association with sugar type, in the presence of marked preferences.

Lateralization or stereotyped foraging behavior?—Lateralization in neural, sensory, and physiological functions is well documented among birds such as Chaffinches (*Fringilla coelebs*; Rogers 1980), canaries, White-crowned Sparrows (*Zonotrichia leucophrys*; Nottebohm 1980), White-throated Sparrows (*Z. albicollis*; Lemon 1973), and Amazon psittacines (Rogers 1980). Occlusion of the left eye affects pecking rates and discriminatory abilities in domestic chickens (*Gallus gallus*; Rogers 1980), whereas the right eye system of food-storing Marsh Tits (*Parus palustris*) is associated with long-term memory storage (Clayton and Krebs 1993, Krebs et al. 1996). The structural bases of these asymmetries are not well documented, but their functional manifestations are numerous enough to have prompted speculation about the advantages of lateralization for foraging birds. Specialization of different hemispheres may "conserve neural circuitry" (Rogers 1980), permitting increased efficiency of memory localization and categorization (Clayton and Krebs 1993). In our study, equal numbers of both sugarbirds and sunbirds preferred left or right-hand feeder positions, and side preferences were independent of feeder position within the cages. Thus, the side preferences that we documented did not result from true lateralization or handedness, but rather from stereotyped foraging behavior.

In a study of three species of hummingbirds, Cole et al. (1982) reported that birds learn more easily to go to a new feeder position ("win-shift learning") than to return to a previously profitable feeder site ("win-stay learning"). They suggested that win-shift learning increases foraging efficiency when a resource is depleted after a single visit, as are hummingbird flowers. In contrast, the nectarivores that we studied preferred to return to the same feeder position. Our feeders offered an infinite, nondepleting food source *sensu* Gass (1978), differing from the artificial flowers offered in the study by Cole et al., which were emptied after a single visit. Sugarbirds and sunbirds may be capable of win-shift learning under different experimental conditions, but the fact that some sugarbirds were reluctant to switch feeders, even

when their favored feeder contained a xylose solution that made them ill, suggests that their stereotyped behavior is to some extent "hard-wired." Cole et al. (1982) suggest that the ease of win-shift versus win-stay learning in a given species is related to the spatial and temporal scale of resource depletion encountered by that species in nature. Such data are lacking for fynbos nectarivores and are crucial for fully understanding the adaptive advantages of their foraging behavior.

Sugar-type preferences.—The preference hierarchy for the three common nectar sugars in Lesser Double-collared Sunbirds (sucrose > hexose mixture = fructose > glucose) corroborates the results of Lotz and Nicolson (1996), demonstrating that these preferences prevail when experimental designs take side biases into account. However, the small number of individuals showing consistent preferences in both trials suggests that this hierarchy is weak. In contrast, sugarbirds have no consistent preferences among the sugars that we tested. Probably for physiological reasons, fynbos nectarivores lack the sucrose aversion that has been documented in other species. Both species that we studied assimilate sucrose as efficiently as they do glucose (>97% efficiency; Lotz and Nicolson 1996, Jackson et al. 1998); therefore, they must have the intestinal disaccharidase sucrose that is a prerequisite for sucrose assimilation. Two species of Australian honeyeaters (Meliphagidae) assimilate sucrose with equally high efficiency (Collins and Morellini 1979, Collins et al. 1980). Sucrose intolerance therefore is not ubiquitous among passerine nectarivores (Lotz and Nicolson 1996), and in Africa it may be restricted to the more frugivorous starlings. For example, Purple-headed Glossy-Starlings (*Lamprotornis purpuriceps*) prefer hexoses to sucrose and probably assimilate sucrose poorly (Malcarney et al. 1994). Among six American and European passerines, two emberizids find sucrose palatable and can assimilate it (Martínez del Río et al. 1988), one bombycillid prefers hexoses but can assimilate sucrose with low (61%) efficiency (Martínez del Río et al. 1989), and four members of the Sturnidae, Muscicapidae, and Mimidae neither like sucrose nor can assimilate it (Schuler 1983, Martínez del Río et al. 1988, Karasov and Levey 1990, Brugger 1992, Malcarney et al. 1994). Significantly, the European and American passer-

ines and the Purple-headed Glossy-Starling are generalized frugivore/nectarivores, and most bird-dispersed fruits are hexose-dominated (Martínez del Río et al. 1988). Comparison of sugar preferences among specialized nectarivores reveals that passerines and hummingbirds have similar tastes.

It is not surprising that Cape Sugarbirds and Lesser Double-collared Sunbirds find sucrose palatable, because it is the dominant nectar sugar in many of the plant species that characterize the fynbos habitat (Barnes et al. 1995, van Wyk and Nicolson 1995). Extremely high floral diversity coupled with low avian diversity in the fynbos probably accounts for the catholic tastes of sugarbirds. Indeed, generalization in pollination systems may be the rule rather than the exception (Waser et al. 1996). Reasons for the sucrose preference shown by sunbirds are unclear. Dietary acclimation to the sugar encountered most recently is unlikely, because all birds were fed on a solution containing equal parts of sucrose, glucose, and fructose for at least three weeks preceding the preference tests, which is ample time for upregulation of transporters and enzymes. Birds may have undergone dietary "imprinting" on the sugar that they encountered most commonly as juveniles, as suggested by Martínez del Río (1990) for hummingbird preferences for sucrose. Little is known about the nature and nectar composition of food plants selected by Lesser Double-collared Sunbirds in the western Cape or elsewhere in their range.

A second and more mechanistic explanation for the preference might be that ingestion of sucrose-rich nectar results in rapid post-ingestion delivery of energy to the intestine, because solutions of high osmotic concentration slow gastric emptying, and a 20% sucrose solution is half the osmotic concentration of a 20% hexose solution (765 mOsm/kg compared with 1,372 and 1,397 mOsm/kg for glucose and fructose, respectively). Gastric emptying of glucose slows with increasing concentration in nectarivorous Rainbow Lorikeets (*Trichoglossus haematodus*; Karasov and Cork 1994), supplying indirect corroboration for this explanation.

Energy density is known to influence ingestion rates of sugar solutions by nectarivores (see below), so we used only 20% (w:w) total sugar solutions in preference tests between different sugar types. A converse approach,

where osmotic concentration rather than energy density of sugar solutions was held constant, revealed that Gurney's Sugarbirds (*Promerops gurneyi*), Malachite Sunbirds (*Nectarinia famosa*), and Black Sunbirds (*N. amethystina*) preferred a 0.25M sucrose solution to equimolar fructose or glucose solutions (Downs and Perrin 1996). These results are not surprising, because nectarivores have long been known to choose solutions of higher concentration to maximize their rate of energy ingestion (Hainsworth and Wolf 1976, Collins and Morellini 1979, Collins et al. 1980, Tamm and Gass 1986, Lloyd 1989, Roberts 1996). A sucrose (disaccharide) solution of a given molarity contains approximately double the solute mass, hence double the energy, of equimolar monosaccharide solutions of glucose or fructose. Net energy absorption rates from different sugar solutions thus are influenced by percentage (w:w) solute concentration, which affects ingestion rate, and by osmotic concentration, which affects gastric emptying rates. In turn, energy absorption rate probably influences a bird's choice of solutions.

Preference tests on Lesser Double-collared Sunbirds reared from hatching on different sugars would reveal whether sucrose preference results from dietary imprinting or from the beneficial effects of ingesting a solution of a lower osmotic concentration. If birds preferred the sugars upon which they were raised, the first explanation would hold but the second would not. If birds preferred sucrose regardless of their rearing conditions, their sugar preferences presumably could have been fixed either by the energetic considerations outlined above, or by coevolution with plants that have sucrose-dominant nectars. Preference tests on birds of this species from different parts of its geographical range might reveal differences among populations in sugar preferences, but such data would be informative only if coupled with flower preference and nectar composition data, which currently are lacking.

The pentose monosaccharide xylose constitutes up to 39% of total nectar sugar among the Proteaceae (van Wyk and Nicolson 1995). Interestingly, however, both of the nectarivores that we studied show a xylose aversion. In Cape Sugarbirds, this was first detectable when xylose constituted 30% of total sugar, a fractional concentration similar to that of nectar that these birds encounter in the wild. Neither

the Cape Sugarbird nor the Lesser Double-collared Sunbird appears able to assimilate xylose (Lotz and Nicolson 1996, Jackson et al. 1998). Therefore, the reason for the presence of xylose in Proteaceae nectar is obscure.

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