Dilute bird nectars: viscosity constrains food intake by licking in a sunbird


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Floral nectars of bird-pollinated plants are relatively dilute. One hypothesis proposed to explain this concerns the difficulty for birds of drinking nectar of high viscosity. We examined the effects of viscosity, separately from those of sugar concentration, on feeding by captive whitebellied sunbirds (Cinnyris talatala). Viscosities of artificial nectar (sucrose solutions ranging in concentration from 0.25 to 1.5 mol/l) were altered with Tylose, an inert polysaccharide. Food consumption was measured over 3 h, and lick frequency and duration were recorded using photodetection devices on feeding apertures too small for the bill but large enough for the extended tongue. Volumetric intake rates (ml/s) were inversely proportional to nectar viscosity, and were similar over the range of sucrose concentrations when viscosity was held constant. Sucrose intake rates (mg/s) remained the same on pure sucrose solutions, but they decreased with increasing viscosity at a constant sucrose concentration. Lick frequencies and tongue loads were reduced at high viscosities, and lick duration increased, which confirms that sunbirds take longer to ingest viscous solutions. Licking behavior was remarkably similar in birds feeding on different sucrose concentrations if viscosity was held constant. Nectar ingestion rate is determined by viscosity; however, total food intake is mainly modulated by sugar concentration. Similar effects of food viscosity have been observed in insects that suck nectar.

Viscosity is a measure of the tendency of a fluid to resist shearing or deformation (43). The viscosity of Newtonian fluids, such as sugar solutions, depends on temperature and chemical composition (25, 41). Sucrose solutions have higher viscosities than glucose or fructose solutions of the same molar concentration, but the differences are much less when concentrations are expressed on a percentage mass basis (41, 44). In addition to the relative proportions of the main nectar sugars, other nectar constituents, such as ions or amino acids, may affect the viscosity. Heyneman (15) used capillary descent times to measure the viscosities of hummingbird nectars and suggested that the presence of nonsugar solutes led to higher values than for equivalent sugar solutions. Nectar temperature also influences viscosity, but concentration has a much greater effect (15, 34).

The tongues of hummingbirds and sunbirds have a bifurcated tip, the edges coiling inward to form open grooves (6, 9, 14). When they lick nectar from flowers, the fluid is loaded onto the tongue by capillary forces (10, 14, 38). Uptake of liquid diets depends on the physical properties of the fluid, morphology of the feeding structures, and the force produced, whether by suction or capillary mechanism (for a review for insects, see Ref. 21). Several authors have used biophysical models to determine the optimal nectar concentration for hummingbirds. For hummingbirds (and other nectarivores) Heyneman (15) proposed that a concentration around 0.85 mol/l would be optimal in the case of large nectar volumes, assuming a steady-state continuous nectar flow. Conversely, Kingsolver and Daniel (20) argued that nectar flow is not steady state if induced by capillarity; rapid tongue movements during licking mean that flow will be discontinuous, and for hummingbirds, they predicted optimal concentrations of 1.15–1.35 mol/l for high-volume nectar pools that require several licks, but 0.65–0.8 mol/l for small volumes that require single licks. Gass and Roberts (13) modeled hummingbird visits to flowers and showed that the optimal nectar concentration increases with temporal scale: the time to complete tongue loading, a licking cycle (inserting the bill, inserting and withdrawing the tongue, and withdrawing the bill) and entire visits to flowers. These models of feeding in avian nectarivores predict that increased viscosity will limit the amount of food ingested per lick, but this has not been tested empirically.

The addition of inert polysaccharides such as cellulose ethers to artificial nectars has enabled researchers to differentiate between the effects of sugar concentration and viscosity on the feeding behavior of insect nectarivores. For example, Josen and Farina (19) fed sucrose solutions with artificially increased viscosity to the hovering hawk moth, Macroglossum stellatarum, and found that both viscosity and sucrose concentration influence the nectar intake rate. On the other hand, the orchid bee Euglossa imperialis feeds at a constant rate when the diet sugar concentration increases from 0.15 to 1.8 mol/l while the viscosity is held at that of a 1.8 mol/l sucrose solution.
at 30°C (2). In this species, which unlike most bees is a suction feeder, viscosity is the major determinant of ingestion rates. The only study to date on nectarivorous birds is that of Stromberg and Johnsen (39), who examined the independent effects of artificial sweeteners, sucrose concentration, and viscosity in field tests of the feeding preferences of black-chinned hummingbirds (Archilochus alexanderi). The authors concluded that a sweet stimulus, rather than the mechanical effect of high viscosity, was required to induce feeding. Sucrose intake rates were not measured directly. The effect of sugar concentration on the licking behavior of nectarivorous birds, however, has been investigated in earlier studies; while tongue load was always inversely proportional to sugar concentration in hummingbirds (14, 36), lick frequencies yielded inconsistent results (8, 14, 36).

In this study, we tested Baker’s hypothesis (1) by assessing the effects of nectar viscosity, separately from those of sugar concentration, on feeding by whitebellied sunbirds, Cinnyris talatala (Nectariniidae). In addition to pure sucrose solutions of different concentrations, we tested the same sucrose concentrations with the viscosity increased with Tylose to that of a 1.5 mol/l solution (constant viscosity series), and a low sucrose concentration with variably increased viscosity (constant concentration series). We hypothesized that licking behavior, and thus intake rates, would be affected by viscosity, rather than sugar concentration. Sugar concentration, on the other hand, was expected to be the feeding stimulus, with birds adjusting their total nectar intake according to its energy content.

**MATERIAL AND METHODS**

**Study animals and their maintenance.** Seventeen whitebellied sunbirds (Cinnyris talatala) were mist-netted in Jan Cilliers Park, Pretoria, South Africa, in 2008 and 2009. Upon capture, body mass (means ± SE) of the 11 males was 8.76 ± 0.14 g and of the six females was 7.92 ± 0.25 g. Birds were housed together in an outdoor aviary at the University of Pretoria Experimental Farm and were moved to individual cages (45 × 45 × 32 cm) in a climate-controlled room (20 ± 2°C) 3 wk prior to experiments. The photoperiod was 12:12-h light-dark, with lights on at 0700. The maintenance diet consisted of 0.63 mol/l sucrose with a nutritional supplement (Ensure, Abbott Laboratories, Johannesburg, South Africa) to provide dietary nitrogen. This diet and supplementary water were provided ad libitum in inverted, stoppered syringes. Birds were released at the site of capture following completion of the study. Experiments were approved by the Animal Use and Care Committee of the University of Pretoria.

**Tongue morphology.** The tongues of one male and one female whitebellied sunbird that had died in captivity were removed and immediately frozen. They were later chemically fixed for 24 h and rinsed in phosphate buffer. After drying in ethanol (30, 50, 70, 90, and 99%) and critical point drying, the tongues were cut into 1-cm sections, mounted on an aluminum board, and gold coated. The tongue sections were examined and photographed using a scanning electron microscope (JSM-5800LV; JEOL, Tokyo, Japan).

**Experimental diets.** The experiment consisted of three test series: a control series (CS), a constant viscosity series (CVS), and a constant sugar concentration series (CCS). The CS consisted of four pure sucrose solutions of 0.25, 0.5, 1, and 1.5 mol/l, which were presented to each bird in random sequence on consecutive days. The CVS consisted of the same four sucrose concentrations, but with the viscosity held equivalent to that of a 1.5 mol/l sucrose solution. In the CCS, birds were fed a 0.25 mol/l sucrose diet throughout, with the viscosity equivalent to that of 0.25, 0.5, 1, and 1.5 mol/l sucrose solutions.

The dynamic viscosities (mPa·s) of all sucrose solutions were determined with an Anton Paar Rheometer (Model Physica MCR 301, Cup-C-PTD200, Spindle-CC27; Advanced Laboratory Solutions, Johannesburg, South Africa), using the RHEOPLUS/32 v.3.00 software package, at 20°C and a shear rate of 60.8 s⁻¹ (automatically maintained by the system). The rheometer was calibrated with pure water as the standard (1.002 mPa·s at 20°C). The viscosity of experimental diets was altered using Tylose H 10000 P2 (SE Tylose & KG, Wiesbaden, Germany, hereafter referred to as Tylose). Tylose is a hydroxyethylcellulose ether (a polysaccharide, molecular weight 10,000 Da) used as a binder or thickener in various foods. It is nonionic and does not alter the nutritional value or density of foods. The amounts of Tylose added to sucrose solutions were estimated by extrapolating from Josens and Farina’s (19) data of kinematic viscosity of sucrose solutions, using a regression equation. Viscosities of test solutions were measured with the rheometer, and adjusted with additional Tylose until the correct amount was determined. All solutions containing Tylose were stirred thoroughly at room temperature, as Tylose was not readily soluble. The amounts of Tylose added and the viscosities of experimental diets are presented in Table 1.

**Experimental procedure.** Birds were trained to feed from the feeding device (mounted outside the cage), which consisted of a hole (1.2 mm in diameter) through a 3-mm thick Perspex plate, highlighted by red nail varnish to attract the bird. A black pipe (diameter: 7 mm), mounted between the Perspex and the feeder, housed a phototransmitter and a photoreceptor set 6 cm apart, on either side of the feeding hole. The hole was big enough to allow for normal food intake, but small enough to force the bird to extend its tongue to feed, since the bill could not be inserted. The photodetection systems were interfaced to a computer, and tongue licks were recorded every 1 ms using custom-designed software. Birds were fed the four sucrose diets of a particular test series in random order on consecutive days. Ambient temperature and light period were the same as during maintenance. Data were recorded for 3 h (0900–1200), since food intake of sunbirds is most stable in the morning (23). Birds were fed their maintenance diet outside the test period to compensate for body mass loss on sugar-only diets (31). At least 10 maintenance days were given between the different test series. Data were obtained from 17 sunbirds for the CS, 16 sunbirds for the CVS, and 15 sunbirds for the CCS.

For each 3-h test period, food intake (g/3 h) was determined by weighing the feeders (and small paraffin-filled trays placed underneath to collect drips), and converted to volumetric intake (ml/3 h) based on the density of sucrose solutions (44). Food intake was measured for 3 h to minimize disturbance of the birds, but it can vary during the 3-h period (23), so we do not present hourly intake data. Sucrose intake (g/3 h) was calculated for each diet. Intake rates (μl/s/g)

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**Table 1. Quantities of Tylose H 10000 P2 added to sucrose solutions to increase viscosities, and dynamic viscosities measured with an Anton Paar rheometer at 20°C, shear rate 60.8 s⁻¹**
or mg/s) were calculated by dividing the volumetric and sucrose intake by the total time spent licking. The start and end time of each tongue lick enabled calculation of lick durations (ms). Lick frequency (licks/s) equaled the number of licks during the 3 h divided by the total time that the bird spent licking. Tongue load (mg) was determined by dividing the 3-h food intake by the number of licks.

Statistical analysis. All data were tested for homogeneity of variance (Levene’s test) and normality (Kolmogorov-Smirnov test). Volumetric and sucrose intake, volumetric and sucrose intake rates, tongue load, lick duration, and lick frequency of each test series were separately subjected to repeated measures ANOVA (RM-ANOVA), with diet being the within-effect factor. These variables were also individually compared between test series using RM-ANOVA, with test series being the within-effect factor. Post hoc comparisons for all RM-ANOVA were conducted with Tukey’s Honestly Significant Difference test for equal sample sizes, followed by a Bonferroni correction for multiple comparisons. To test for the effect of sex on licking variables, we subjected tongue load, lick duration, and lick frequency of males and females in the control series to Mann-Whitney U-tests. Although data were normally distributed, the more conservative nonparametric test was chosen due to the problems associated with distribution estimation from small sample sizes (45). Level of significance was α = 0.05; data are presented as means ± SE.

RESULTS

Food intake. Sunbirds licked the sucrose solution with only their tongue tip (Fig. 1) immersed. Volumetric intake rate (μl/s) was inversely proportional to the concentration of pure sucrose solutions (CS; $F_{3,48} = 6.40, P < 0.001$), but it remained similar when the same concentrations were increased to a constant viscosity of 1.5 mol/l (CVS; $F_{3,45} = 0.61, P = 0.61$; Fig. 2A). When a low sucrose concentration (0.25 mol/l) was made up to different viscosities (CCS), volumetric intake rates decreased with increasing viscosity ($F_{3,42} = 3.92, P = 0.01$; Fig. 2A). Volumetric intake rates on CS solutions were significantly greater than those on the corresponding CVS and CCS solutions ($F_{2,28} > 3.34, P < 0.05$), except on the highest concentration/viscosity (1.5 mol/l; $F_{2,28} = 3.22, P = 0.06$). Total volumetric intake (ml/3 h; not shown) decreased with increasing sucrose concentration in the CS and the CVS ($F_{3,48/45} > 13.67, P < 0.001$), as expected from compensatory feeding. Surprisingly, volumetric intake also decreased with increasing viscosity in the CCS, despite the constant sucrose concentration ($F_{3,42} = 76.69, P < 0.001$). Volumetric intake of same concentration/same viscosity diets differed between the three test series ($F_{2,28} > 21.31, P < 0.001$), being highest in the CCS and lowest in the CVS, but did not differ when the same diet was fed in different test series ($P = 0.99$), indicating that feeding remained regular between test series. Birds spent on average 4.60 ± 0.97 min feeding during the 3-h test period.

Sucrose intake rate (mg/s) did not differ between CS solutions ($F_{3,48} = 1.83, P = 0.15$) but increased with increasing sucrose concentration on the CVS diets ($F_{3,45} = 6.45, P < 0.01$; Fig. 2B). For the CCS, sucrose intake rate declined with increasing viscosity ($F_{3,42} = 3.92, P = 0.01$; Fig. 2B). Sucrose

Fig. 1. Scanning electron microscopy photograph of the bifurcated tongue tip of *Cinnyris talatala*. Only the tongue tip was immersed in the test solution during our experiments.

Fig. 2. Effect of concentration and viscosity of sucrose solutions on volumetric intake rate (A; μl/s) and sucrose intake rate (B; mg/s) by *Cinnyris talatala* consuming three different test series (means ± SE). Bars on the left represent the control series (CS), in which birds were fed pure sucrose solutions of different sugar concentrations: 0.25 mol/l (black bar), 0.5 mol/l (white bar), 1 mol/l (dark gray bar), and 1.5 mol/l (gray bar). The constant viscosity series (CVS) is presented in the middle, where birds were given the same sucrose concentrations but viscosity of each solution was increased with Tylose to that of 1.5 mol/l sucrose [0.25 mol/l (black bar), 0.5 mol/l (white bar), 1 mol/l (dark gray bar), and 1.5 mol/l (gray bar)]. The constant concentration series (CCS) is shown on the right, where sucrose concentration of all solutions was 0.25 mol/l, with increasing viscosity [viscosities of 0.25 mol/l (black bar), 0.5 mol/l (white bar), 1 mol/l (dark gray bar), and 1.5 mol/l (gray bar)]. Significant differences within test series are indicated by asterisks (*$P \leq 0.05$, **$P < 0.01$, ***$P < 0.001$). Statistical differences between test series are omitted for clarity.
intake rate was greater on the CS diets than on the corresponding CVS and CCS solutions ($F_{2,28} = 4.53, P < 0.02$), except on the highest concentration/viscosity (1.5 mol/l; $F_{2,28} = 3.07, P = 0.06$). Total sucrose intake (g/3 h; not shown) differed significantly between the CS concentrations ($F_{3,48} = 17.02, P < 0.001$), with birds ingesting less sucrose on the 0.25 mol/l diet than on more concentrated diets ($P < 0.001$). Sucrose intake also increased with increasing concentration on the CVS diets ($F_{3,45} = 165.04, P < 0.001$), while it decreased with increasing viscosity of the CCS diets ($F_{3,42} = 76.69, P < 0.001$). Sucrose intake was higher on CS diets than on corresponding CVS and CCS solutions ($F_{2,28} = 62.39, P < 0.001$), except when birds fed on the same test diets ($P = 0.99$).

$Licking behavior$. Tongue load (mg) decreased with increasing CS diet concentration ($F_{3,48} = 14.66, P < 0.001$) and increasing CCS diet viscosity ($F_{3,42} = 2.80, P = 0.05$), while it remained similar on the range of CVS diets ($F_{3,45} = 0.21, P = 0.89$; Fig. 3A). Tongue load was higher on 0.25 and 0.5 mol/l CS diets than on corresponding CVS diets ($F_{2,28} > 4.08, P < 0.03$), while it did not differ between the remaining diets ($F_{2,28} = 1.72, P > 0.20$).

Lick duration (ms) increased with increasing sucrose concentration of CS diets ($F_{3,48} = 3.62, P = 0.02$), while it was similar on all CVS diets ($F_{3,45} = 0.08, P = 0.97$) and on all CCS diets ($F_{3,42} = 1.20, P = 0.32$; Fig. 3B). Lick duration was longer on 0.25 and 0.5 mol/l CVS diets than on corresponding CS and CCS diets ($F_{2,28} > 4.14, P < 0.03$), but the remaining diets did not differ ($F_{2,28} < 2.03, P > 0.15$).

Lick frequency (licks/s) decreased with increasing sucrose concentration in the CS ($F_{3,48} = 3.87, P = 0.01$) and was similar on all CVS diets ($F_{3,45} = 0.82, P = 0.49$; Fig. 3C). Lick frequency tended to decrease, but not significantly, with increasing viscosity in the CCS ($F_{3,42} = 2.36, P = 0.08$; Fig. 3C). Birds licked faster on CS diets than on corresponding CVS and CCS diets ($F_{2,28} > 3.39, P < 0.05$), except when feeding on diets of the same concentration or viscosity in different test series ($P > 0.14$). There was no effect of sex on licking behavior. In the control series, males and females did not differ in terms of tongue load, lick duration, or lick frequency ($U > 25.0, P > 0.45$).

**DISCUSSION**

Many factors influence nectar extraction by avian nectarivores: bill length and curvature; floral characters such as length, curvature, and orientation; and nectar properties, such as volume, concentration, and sugar composition (7, 28). Where nectar concentration is concerned, the addition of small amounts of the inert polysaccharide Tylose has allowed us to assess whether sunbird consumers are responding to the sweetness or viscosity of nectar. Our study shows conclusively that effects of concentration and viscosity on nectar consumption by sunbirds and how these variables affect licking behavior. We then compare our findings to those for some insect nectar consumers, and consider the implications for the nectar properties of bird-pollinated flowers.

Food intake on pure sucrose solutions from 0.25 to 1.5 mol/l confirmed the compensatory feeding previously reported in this species (31), where volumetric intake increases with decreasing sucrose content of the nectar to maintain a constant energy intake. Although sunbirds ingested less sucrose over 3 h on the 0.25 mol/l diet than on more concentrated diets, they have been shown to compensate perfectly when fed this diet concentration over a whole day (31). Sunbirds feed intermittently, and...
measurement of actual feeding time allowed the calculation of volumetric intake rates, which were inversely proportional to concentration, and sucrose intake rates, which peaked (although not significantly) at an optimal concentration of 1 mol/l sucrose. This represents a balance between the low energy content at low concentrations and the mechanical effect of high viscosity at high concentrations. Short-term adjustment of food intake in this species occurs through changes in feeding frequency rather than feeding duration (23). Whitebellied sunbirds rapidly detect changes in nectar sucrose concentration and adjust their feeding frequency within a few minutes of a concentration change (22). Pair-wise tests of the concentration preferences of whitebellied sunbirds show that they prefer the higher concentration up to 1 mol/l for both sucrose and equicaloric hexose solutions, while they generally tend to prefer the lower concentration above 1 mol/l (24). This preferred concentration, although higher than that of most sunbird nectars (17), is that which maximizes energy intake rates. A similar pattern was found for rufous hummingbirds (Selasphorus rufus), which prefer more concentrated nectars over dilute ones, but discriminate against very concentrated solutions (40).

For sunbirds feeding on the CVS solutions, with low to moderate sucrose concentrations and the viscosity of 1.5 mol/l sucrose, volumetric intake rates and licking behavior remained similar. Volumetric intake rates, tongue load, and lick frequency were considerably reduced compared with those on the corresponding pure sucrose solutions, while lick duration was higher. Volumetric intake rates and licking behavior on the CCS solutions showed a similar decline with increasing viscosity to that observed on pure sucrose solutions. This finding supports the hypothesis that licking behavior, and thus intake rates, is affected by viscosity, and not by sugar concentration. Higher sugar concentrations lead to higher energy intake rates, except at the highest sucrose concentration (1.5 mol/l), simply because it takes longer to ingest this viscous solution.

Results for the CVS solutions also demonstrate that the birds responded to sucrose concentration as the feeding stimulus: they consumed more of the dilute diets, although the viscosities of the solutions were equal. On the lowest sucrose concentration, however, volumetric and sucrose intake were lower on very viscous solutions than on the pure 0.25 mol/l diet (CCS), indicating that intake rate was constrained by high viscosity. The low concentrations of thickening agents used in our study should not affect sweetness perception. Similarly, the addition of sodium carboxymethyl cellulose to increase viscosity did not stimulate feeding by black-chinned hummingbirds in three-way preference tests under field conditions (39), but higher concentrations of cellulose ethers have been observed by food scientists to reduce the perceived sensitivity to volatile and nonvolatile components in humans (16).

Our study is the first to investigate the separate effects of nectar concentration and viscosity on the licking behavior of nectarivorous birds. The effect of pure sugar solutions of different concentrations has been examined in earlier studies. Roberts (36) recorded the licking behavior of a single rufous hummingbird using a photodetection system and found that the bird decreased its lick frequency and tongue load with increasing sucrose concentration, which is in agreement with our finding for sunbirds. Lick frequencies in sunbirds (up to 40 licks/s on a dilute diet) were higher than those measured in early studies of avian nectarivores, probably because the video recordings underestimated lick frequencies through insufficient resolution (10, 14, 38). Regardless of the actual values, it appears that nectar intake depends more on tongue load than on the lick frequency. At higher concentrations, grooves on the tongue are likely to fill only partially with nectar because the solutions are too viscous for efficient capillarity. Incomplete loading is apparent even with lower viscosities and high-volume feeders; it is not profitable for birds to load their tongues fully because flow rate decreases as nectar moves up the grooves (20). The decline in tongue load with increasing concentration of pure sugar solutions is in agreement with findings for blue-throated (Lampornis clemenciae) and black-chinned hummingbirds (14) and a rufous hummingbird (36). In addition to concentration, nectar volume also influences ingestion: tongue load, and thus sugar intake rate, increases with nectar volume in both hummingbirds and honeyeaters (7, 27); the latter have brush tongues that also collect nectar by capillarity (33). Decreasing corolla length has the same effect (7, 14); in both cases, the contact between tongue and nectar is increased, and thus the volume collected per lick. The models of Gass and Roberts (13) assumed that only the tip of the tongue contacts the nectar pool, which was also true for our experimental setup. This is more ecologically realistic because the mean nectar volume in sunbird and hummingbird flowers is only 10–30 µl (17).

Viscosity modification with Tylose has also been used to dissociate the effects of concentration and viscosity on food intake of insect nectarivores. Ingestion volumes and feeding durations have been recorded for single uninterrupted meals, thus providing data on volumetric intake rate and sucrose intake rate. There are remarkable similarities in the responses of insects and sunbirds to CVS and CCS solutions, in spite of different modalities of fluid feeding. In the hovering hawk moth Macroglossum stellatarum, volumetric intake rate is reduced compared with pure sucrose solutions when viscosity remains constant at that of 1.8 mol/l sucrose (CVS), although the effect of concentration is still apparent, and volumetric intake rate is reduced when sucrose concentration is kept at 1 mol/l and the viscosity progressively increased (CCS) (19). Sucrose intake rate of the moths is maximal at about 1.14 mol/l. In an orchid bee (Euglossa imperialis), volumetric intake rate decreases when viscosity increases from 2 to 80 mPa·s (at 30°C), while the sucrose concentration is held at 0.8 mol/l (CCS), but remains constant when concentration increases from 0.15 to 1.8 mol/l, while the viscosity is held at 10.2 mPa·s (the viscosity of a 1.8 mol/l sucrose solution at 30°C) (CVS) (2). Sucrose intake rate is maximal at 1.15 mol/l. In hawk moths, orchid bees and sunbirds, viscosity ensures that volumetric intake rates are constant on CVS solutions [with the exception of M. stellatarum consuming 1.35 mol/l CVS with viscosity equivalent to 1.8 mol/l sucrose; (19)]. In all three species, volumetric intake rates on CCS solutions decline with increasing viscosity. The long-tongued orchid bees suck nectar, and their maximum sucrose intake rates at 1.15–1.35 mol/l are lower than those of lapping bees (3); this confirms the prediction (20) that a shift from lapping or licking to suction feeding will lead to greater dependence on viscosity. The trophallactic food transfer of honeybees (which involves regurgitation, as well as ingestion) is also slowed by artificial increases in viscosity (42), as are feeding rates in the nectarivorous ant Camponotus mus (26). However, nectar intake of social insects
may depend on motivational factors, as well as physical limitations (11).

Most nectars are only slightly more viscous than pure sugar solutions of the same concentration (15). Salts and amino acids typically occur at low concentrations in floral nectars, but little information is available for other constituents (32). The impact of nonsugar solutes and fallen pollen on nectar viscosity is not known. Small quantities of certain solutes, especially macromolecules, may have a large effect on viscosity of sugar solutions (25), as seen in the jelly-like nectar of some vertebrate-pollinated flowers (18, 37). Nectars may be dominated by sucrose or its component hexoses, and there has been considerable interest in whether nectar sugar composition is determined by pollinator preferences or plant phylogeny (17, 32). Viscosity differences between sucrose solutions and equimolar glucose-fructose mixtures are slight, so there is no advantage in terms of viscosity to feeding on one or the other sugar type (5, 12). Hexose-dominated nectars tend to be dilute, because hydrolysis of sucrose increases nectar osmolality, thus drawing additional water into the nectar (30). Such nectars are characteristic of flowers adapted for generalized bird pollinators, which have high volumes (40–100 μl), low sugar concentrations (around 0.3 mol/l), and low sucrose levels compared with those visited by specialist hummingbirds and sunbirds (4, 17). While viscosity constraints help to explain the low sugar concentrations of bird nectars, in general, they do not easily explain the exceptionally dilute hexose nectars consumed by short-billed generalist birds. However, differences in nectar viscosity between these bird pollination systems are slight compared with those between bird and bee nectars (35), owing to the steep increase in viscosity as a function of sugar concentration (32, 41).

**Perspectives and Significance**

Why are bird nectars so dilute? More than three decades ago, it was proposed that low concentrations are necessary for efficient extraction of nectar by birds (1), but experimental evidence has been lacking. The present study provides strong support for Baker’s (1) hypothesis that the most efficient energy intake occurs at sugar concentrations that represent a compromise between low energy content and high viscosity. Therefore, nectarivorous birds should favor lower nectar concentrations. It remains to be tested whether this also applies to birds with high metabolic requirements or birds in negative energy balance, which may feed on more concentrated nectar. Lastly, in using unlimited volume feeders, we have considered the effects of nectar concentration in isolation from volume. The role of avian nectarivores in the evolution of nectar traits will depend not only on low concentrations, but also on the copious nectar volumes that are characteristic of bird-pollinated flowers.

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**REFERENCES**


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**DISCLOSURES**

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