URINARY CONCENTRATING ABILITY OF A NECTARIVOROUS BIRD, THE RUBY-THROATED HUMMINGBIRD (*ARCHILOCHUS COLUBRIS*)

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Hummingbirds rely primarily on consumption of floral nectar to meet their high energy requirements, and as a consequence they have among the highest rates of water turnover of any vertebrate, terrestrial or aquatic (Beuchat, Calder, and Braun, Physiol. Zool. 63: 1059-1081, 1990). Not surprisingly, the morphology of the hummingbird kidney differs in some significant ways from that of other birds. The avian kidney typically contains two types of nephrons, looped and loopless. The looped nephrons, which are organized in clusters called medullary cones, resemble the short-looped nephrons of mammals, with a well-developed loop of Henle but without the segment of thin ascending limb found in the longest mammalian nephrons. These nephrons play a key role in generating the medullary osmotic gradient that allows concentration of the urine. The loopless avian nephrons resemble those of reptiles; they lack a loop of Henle and, because they are oriented at right angles to the collecting ducts, are thought to play no role in urine concentration (Braun and Dantzler, Am. J. Physiol. 222: 617-629, 1972). The kidneys of hummingbirds, on the other hand, contain few looped nephrons, and the medullary tissue amounts to only 2% of the total kidney mass (Casotti, Beuchat, and Braun, J. Zool., in press). We would expect, therefore, that the urinary concentrating ability of hummingbirds might be very limited.

The goal of this experiment was to assess the urinary concentrating ability of hummingbirds under conditions in which they may need to minimize excretory water loss to remain in water balance. To do this, birds were fed sugar solutions with concentrations from 0.2 M to 1.6 M. The most dilute diet should provide a large excess of water for a bird consuming enough food to be in energy balance, so excreted urine should be very dilute. When birds are fed the most concentrated diet, they have very low rates of water intake; to avoid dehydration they may need to minimize excretory water loss by concentrating the urine.

Ruby-throated hummingbirds (*Archilochus colubris*; n=7) were captured in Hancock County, ME and maintained singly in the laboratory in cages adequate for flight on a maintenance diet of Nektar Plus (Necton, Inc.). Body mass of the birds averaged 3.1 g. The feeder on each cage was filled with the test diet in the evening after lights out so it would be available to the birds when they awoke in the morning (about 0630 h) of the day of each experiment. Six diet concentrations were used (0.2 M, 0.3 M, 0.7 M, 1.0 M, 1.3 M, and 1.6 M, as total molar concentration of component sugars), in which the sugar composition was 2:1:1 of sucrose, glucose, and fructose, respectively. This resembles the sugar composition of the floral nectar on which the birds typically feed in the wild (Baker and Baker, *Handbook of Experimental Pollination Biology*, Chicago: Univ. Chicago Press, 131-170, 1981). Diets were presented to the birds in random order. Ambient temperature during the experiments averaged 23 °C (± 1 °C).

Experiments were conducted from 1100 h to 1500 h. Food consumption was quantified by weighing each feeder (± 0.0005 g) at the beginning and end of the 4 hour experimental period. The change in mass of a control feeder with the same solution was used to correct for evaporation. Urine samples were collected within 5 min of excretion from a plastic sheet on the floor of each cage using a glass capillary. The samples were transferred to microcentrifuge tubes, quickly frozen in a bath of dry ice and alcohol, and stored at -70 °C until analysis. Osmolality of thawed and thoroughly mixed urine was determined using a Wescor 5500 vapor pressure osmometer with a thermocouple head specially selected for linearity at low osmolalities. If the thermocouple was kept scrupulously clean and the instrument carefully calibrated, my particular instrument could accurately measure osmolality down to 0-3 mmol/kg H_2O (± 1 mmol/kg H_2O; SI units for osmolality).

Food consumption of ruby-throated hummingbirds fed the most dilute diet, 0.2 M sugar, was extremely high, amounting to almost 50% of body mass per hour (Fig. 1a). This was 6 times greater than the rate of consumption on 1.6 M sugar, the most concentrated diet.

Birds fed the most dilute diet (0.2 M) produced voluminous amounts of extremely dilute urine, with an osmolality that averaged only 10 mmol/kg H_2O (Fig. 1b). Urine osmolality progressively rose as the sugar concentration of the diet increased from 0.2 M to 1.3 M.

At the highest food concentration (1.6 M), birds excreted so little urine that I was able to collect enough for analysis from only two birds; these two samples had osmolalities of 28 and 114 mmol/kg H_2O, with the latter being the highest value measured in the experiment.

Water-stressed birds are typically able to produce hyperosmotic urine, with osmolalities up to about twice that of plasma (Goldstein and Braun, Am. J. Physiol. 256: R501-R509, 1989). The highest urine osmolality measured in ruby-throated hummingbirds, on the other hand, was only about a third that of plasma. Rather than producing a more concentrated urine to mitigate dehydration, the hummingbirds ceased water excretion entirely. The apparent inability of hummingbirds to concentrate their urine when water-stressed is consistent with the structure of their kidney, which lacks the well-developed morphological features associated with the concentrating kidneys of other birds (Casotti, Beuchat, and Braun, J. Zool., in press).

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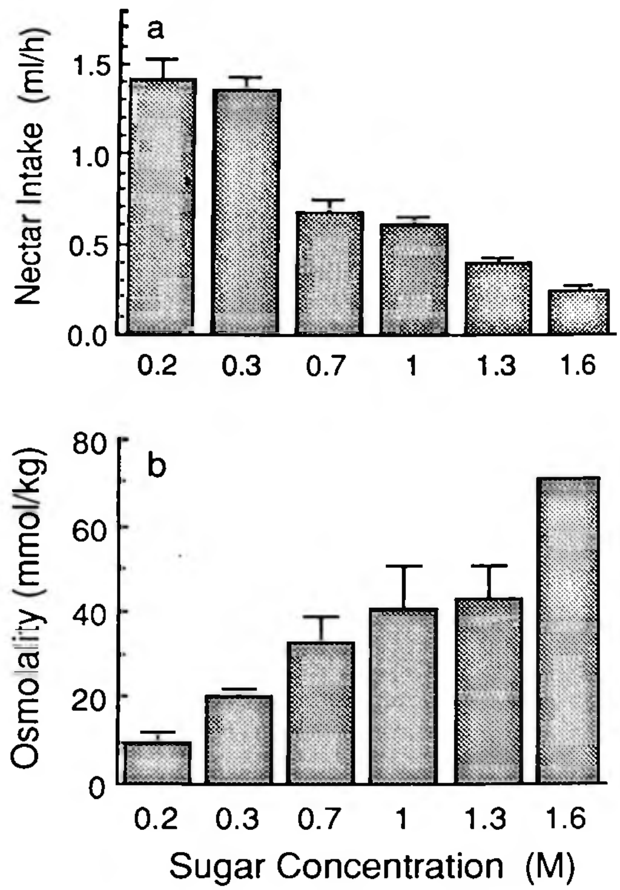

Figure 1. Rate of food consumption (a) and urine osmolality (b) as a function of dietary sugar concentration. Error bars are ± 1 SE.