Water management in nectar-feeding birds

Susan W. Nicolson
Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

NECTARIVORY IS WIDESPREAD in birds, but best known in three unrelated families on different continents: the American hummingbirds, Australasian honeyeaters, and the sunbirds of Africa and Asia. Bird pollinators require substantial nectar rewards and their flowers produce copious nectar, which is, however, more dilute than that of insect-pollinated flowers. On average, the nectars of bird flowers are 75–80% water (14). Variation in nectar concentration within and between plant species leads to compensatory feeding by birds; to maintain constant energy intake, they increase volumetric intake in response to diet dilution (9). On very dilute nectars, daily water gains of several times body mass have been measured in all main lineages of avian nectar feeders (2, 3, 10). Elimination of the surplus water must occur through evaporative and excrery routes, and it has usually been assumed that excretion is most important. Beuchat et al. (1) hypothesized that hummingbirds may shunt water through the gastrointestinal tract to reduce renal water loading, but broad-tailed hummingbirds (Selasphorus platycercus) were found to absorb all dietary water (10).

In this issue of American Journal of Physiology-Regulatory, Integrative and Comparative Physiology, Hartman Bakken and Sabat (7) have used pharmacokinetic techniques to examine the roles of both the gastrointestinal system and kidneys in handling excess water in a South American hummingbird (Sephanoides sephanoides). Water intake during the experiment was easily manipulated by varying dietary sugar concentrations. Two markers, $^3$H$_2$O and L-[14C]glucose, were injected simultaneously in the pectoralis muscle of six tiny male hummingbirds (average mass 5.3 g). Single samples of blood and ureteral urine were collected together with freshly voided excreta samples over a period before and after the overnight fast. The fraction of absorbed water was calculated from the amount of $^3$H$_2$O eliminated in body water production. Glomerular filtration rate (GFR) and fractional water reabsorption ($f_R$) were calculated from the amount of L-[14C]glucose injected, its concentration in ureteral urine and blood, and its rate of elimination in the excreta. This technique enabled the researchers to look at the integration of renal and intestinal systems, an approach neatly illustrated in Fig. 2 of their report (7). Intestinal water absorption was found to be unresponsive to water intake, as in S. platycercus. GFR was also unaffected by water intake, so water regulation appears to depend mainly on modulation of $f_R$ in the hummingbird kidney.

Hovering hummingbirds have higher energy requirements and more need of water shunting than sunbirds: on a diet of 0.29 M sucrose, the food intake of broad-tailed hummingbirds and Palestine sunbirds reaches 5.4 and 2.2 times body mass, respectively (11). However, unlike the two hummingbird species now examined, it is Palestine sunbirds (Nectarinia osea) that are able to modulate intestinal water absorption according to diet concentration. On dilute diets, two thirds of the ingested water may bypass their kidneys by not being absorbed (11). This explains why sunbirds are able to cope with more dilute nectars than hummingbirds (13, 14). Obviously, data on more bird species are necessary. Water shunting requires rapid absorption of sugars, amino acids, and electrolytes from the ingested nectar. Elimination of nonabsorbed water with urine through the cloaca, rather than postrenal modification of the urine, may be the cause of the lower solute concentrations measured in excreted fluid than in ureteral urine (12).

Urine production can increase by the following two mechanisms: an increase in GFR or a decrease in $f_R$ in the kidney. Both glomerular and tubular responses in birds are mediated by decreasing levels of the antidiuretic hormone arginine vasotocin (4). In Palestine sunbirds, $f_R$ is also more sensitive to water status than GFR (12). The same is true of a large honeyeater, the 100-g red wattlebird Anthochaera carunculata (5). Thus variation in $f_R$ seems to be important for management of water excess in all three lineages of nectarivorous birds. However, filtration becomes important during fasting periods, when nectar feeders are subject to dehydration rather than diuresis; two hummingbird species have now been shown to reduce their GFR dramatically at night (6, 7). This complete cessation of filtration is presumed to be a water conservation mechanism linked with the inability of hummingbird kidneys, but not those of sunbirds, to produce concentrated urine (3, 8).

While the focus above has been on water processing by intestinal and renal systems, even less is known of evaporative water losses (EWL) in nectar-feeding birds. Most studies of avian EWL have been carried out in a thermoregulatory context. EWL is modulated, and its partitioning between cutaneous and respiratory routes is altered, by heat stress (16), and the same may be true of osmoregulatory stress. Hartman Bakken and Sabat (7) used their pharmacokinetic models to estimate hummingbird EWL and obtained a low and variable value that appeared trivial in magnitude compared to dietary water uptake. However, evaporation cannot be discounted as a route for dealing with excess water. When EWL is calculated as the difference between dietary water intake and excretory output, it is found to increase substantially on dilute diets (3). In fasted Anna’s hummingbirds (Calyptrine anna), Powers (15) measured the highest mass-specific EWL of any endothermic vertebrate. Direct measurements of EWL while birds are feeding on nectar are complicated by the chronic diuresis, but are sorely needed.

REFERENCES