ORNITOLOGIA NEOTROPICAL 19 (Suppl.): 501–509, 2008

THE MECHANISMS AND ECOLOGY OF WATER BALANCE IN HUMMINGBIRDS

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Resumen. – Los mecanismos y ecología del balance hídrico en picaflores. – Los picaflores confrontan un dilema: cuando se alimentan, tienen tasas muy altas de ingestión de agua y deben eliminarla; sin embargo, cuando ayunan, su capacidad de eliminar agua los hace susceptibles a la deshidratación. A pesar de que el néctar es principalmente agua, los picaflores pueden deshidratarse cuando ingieren néctares moderadamente concentrados ¿Qué mecanismos usan los picaflores para mantener el balance hídrico? Para evitar la sobre-hidratación los picaflores utilizan dos procesos renales, de los cuales el más importante es la reducción de la reabsorción. Sin embargo, la tasa de filtración glomerular parece responder a la carga de agua en algunas circunstancias. Para mitigar la deshidratación durante el ayuno, los picaflores reducen, y hasta cesan, la filtración glomerular. Aunque esta estrategia les permite conservar agua al reducir las perdidas en orina, las tasas de evaporación respiratoria sugieren que los picaflores se deshidratan durante ayunos naturales nocturnos. Es poco claro si los picaflores pueden regular la tasa de perdida de agua por evaporación en respuesta al estado hídrico. De los ocho linajes de aves que han evolucionado el hábito nectarívoro independientemente, los mecanismos de balance de agua están mejor estudiados entre los picaflores. A pesar de que más investigación es necesaria para entender los patrones evolutivos del balance hídrico, los estudios disponibles han revelado convergencia y diversidad en los procesos fisiológicos que las aves nectarívoras usan para resolver los desafíos de osmoregulación que presentan sus dietas.

Abstract. – Hummingbirds are confronted with an osmoregulatory dilemma: when feeding, their high rates of water intake require them to eliminate ingested water quickly; yet, during fasts, their capacity to eliminate water makes them susceptible to dehydration. Indeed, although their food is mostly water, hummingbirds may even dehydrate when they are feeding on moderately concentrated nectars. What mechanisms then do hummingbirds use to maintain water balance? To avoid overhydration, hummingbirds rely on two renal processes, the most important of which is to reduce water reabsorption; however, glomerular filtration rate (GFR) appears to be responsive to water loading under some circumstances. To mitigate dehydration during fasts, hummingbirds reduce, even cease, GFR. Although this strategy conserves body water by reducing losses in urine, rates of evaporative water loss suggest that hummingbirds still dehydrate during natural, overnight fasts. At present, however, it is unclear if hummingbirds are able to regulate evaporative water losses in response to hydration status. Of the eight avian lineages that independently evolved specialized nectar-feeding, the mechanisms of water balance are best understood in hummingbirds. Although more work in other lineages is needed to understand the evolutionary patterns of water balance strategies, studies to date have revealed both convergence and diversity in the physiological processes that nectar-feeding birds use to meet the osmoregulatory challenges resulting from their diet. *Accepted 2 December 2007.*

Key words: Evaporative water loss, glomerular filtration rate, hummingbird, nectarivory, osmoregulation, renal function.

THE OSMOREGULATORY QUANDARY POSED BY NECTARIVORY

In order to maintain water balance, hummingbirds (Trochilidae) must overcome two diametrically opposed challenges. First, as a consequence of ingesting multiples of their body mass per day in water (Beuchat *et al.* 1990, Martínez del Rio *et al.* 2001), hummingbirds must eliminate ingested water rapidly in order to avoid overhydration (Almond *et al.* 2005). During fasting periods, however, hummingbirds are confronted with the antithetical challenge. Because of their high mass-specific evaporative water loss rates (Powers 1992) and inability to form hyperosmotic urine (Lotz & Martínez del Rio 2004), fasting hummingbirds lose body water quickly and are prone to dehydration. Estimates have suggested that the rate of evaporative water loss in hummingbirds is roughly 2% of total body water each hour during non-feeding periods (Hartman Bakken & Sabat 2007), which makes mitigating water losses during fasts equally important to eliminating water excesses during feeding.

What mechanisms do hummingbirds use to resolve this quandary? Here, we review how both the intestinal and renal systems in hummingbirds function to accomplish water balance. We also discuss how evaporative water loss affects water homeostasis in feeding and fasting hummingbirds. To close, we consider what laboratory measurements suggest for the water requirements of hummingbirds in the wild and examine how the physiological processes that hummingbirds use to maintain water balance compare to those used by other nectar-feeding birds. Although this article is concerned with hummingbirds in general, we emphasize the Green-backed Firecrown (*Sephanoides sephanoides*) because it is the only nectar-feeding vertebrate, hummingbird or otherwise, for which a complete water budget has been experimentally constructed (Table 1; Hartman Bakken & Sabat 2006).

OVERHYDRATION AVOIDANCE

In their seminal paper, Beuchat *et al.* (1990) introduced physiological ecologists to the overhydration danger that confronts hummingbirds. In it, they hypothesized that hummingbirds would reduce the fraction of dietary water absorbed in the intestinal tract as water intake rates increased (Beuchat *et al.* 1990). Such a response, although unprecedented at the time in vertebrates (Powell 1987, McWhorter *et al.* 2003), would elegantly explain how hummingbirds avoid overhydration: rather than relying on the kidney to eliminate excessive volumes of water, a significant proportion of ingested water would simply be passed through the gut and excreted.

The first test of Beuchat *et al.*'s (1990) regulated water absorption hypothesis was in the North American Broad-tailed Hummingbird (*Selasphorus platycercus*). There was, however, no evidence to support the conjecture: independent of water intake rate, dietary water absorption was 78 ± 15% (mean ± SD, n = 23; Fig. 1; McWhorter & Martínez del Rio 1999). A number of years later, this test was repeated in the Green-backed Firecrown, a hummingbird distributed in Chile and Argentina. Even though this species ingested up to ~25% of its body mass per hour in water

TABLE 1. Water budget for the Green-backed Firecrown (*Sephanoides sephanoides*; n = 6). These data were obtained in captive hummingbirds feeding voluntarily during the evening. Relationships were determined using standard least squares linear regression with water intake rate (mL h^{-1}) as the independent variable; if there was no relationship between the response variable and water intake rate, the value of the response variable is reported as mean ± SD. Data are from Hartman Bakken & Sabat (2006).

Response variables	Relationship or values
Fractional dietary water absorption	0.91 ± 0.08
Water flux (mL h^{-1})	$y = -0.04 + 0.84x$
Fractional body water turnover	$y = -0.02 + 0.29x$
Metabolic water production rate (mL h^{-1})	0.07 ± 0.01
Renal water loading rate (mL h^{-1})	$y = 0.09 + 0.86x$
Glomerular filtration rate (mL h^{-1})	2.08 ± 0.56
Fractional water reabsorption	$y = 0.75 - 0.11x$
Water excretion rate (mL h^{-1})	$y = 0.41 + 0.47x$
Total evaporative water loss (mL h^{-1})	0.07 ± 0.32

(0.27–1.31 mL h^{-1}), water absorption in the intestinal tract was high (mean = 91%, SD = 8%, n = 6), and independent of water intake (Fig. 1; Hartman Bakken & Sabat 2006).

These findings do not offer support for the osmoregulatory role of the intestinal system hypothesized by Beuchat *et al.* (1990); however, they indicate that, after insensible water losses are discounted, the renal system is chiefly responsible for eliminating excess ingested water in hummingbirds. Therefore, to understand overhydration avoidance in hummingbirds, studies have focused on the rate of glomerular filtration (GFR) and water reabsorption in the kidney. In order for GFR to be considered responsible for eliminating excess ingested water, it must be 1) greater in hummingbirds compared to non-nectarivorous birds, and/or 2) responsive to water loading. The experimental evidence for these criteria is, however, weak: compared to birds with other dietary habits, the GFRs of nectar-feeding birds are not exceptionally high and GFR has only been shown to increase with increasing water intake during the middle of the day in Broad-tailed Hummingbirds (Hartman Bakken *et al.* 2004).

Although increasing GFR to eliminate excess body water may be important in some circumstances, decreasing water reabsorption appears to be the mechanism that hummingbirds rely on to prevent overhydration. In both Broad-tailed Hummingbirds (Hartman Bakken *et al.* 2004) and Green-backed Firecrowns (Hartman Bakken & Sabat 2006), the fraction of water reabsorbed in the kidney decreases as water intake rates increase (Fig. 2). These low water reabsorption values indicate that hummingbirds possess efficient renal water elimination capacities; yet, when body water needs to be conserved (i.e., night), the intercepts of these relationships are ominous: they suggest that hummingbirds lose 11–25% of filtered body water to urine when water intake rates are zero (Fig. 2; Hartman Bakken *et al.* 2004, Hartman Bakken & Sabat 2006). We discuss dehydration in detail later, but it is worthwhile to point out that birds can recover urinary water in the lower intestinal tract (Braun 1993, Goldstein & Skadhauge 2000).

Because of their diminutive body sizes (Fig. 4 in Fleming *et al.* 2004, and references there) and high mass-specific metabolisms (Suarez 1992), evaporative water loss is also an important osmoregulatory consideration in hummingbirds (Hartman Bakken & Sabat 2007). Despite this, the influence of evaporative water loss on water balance in humming-

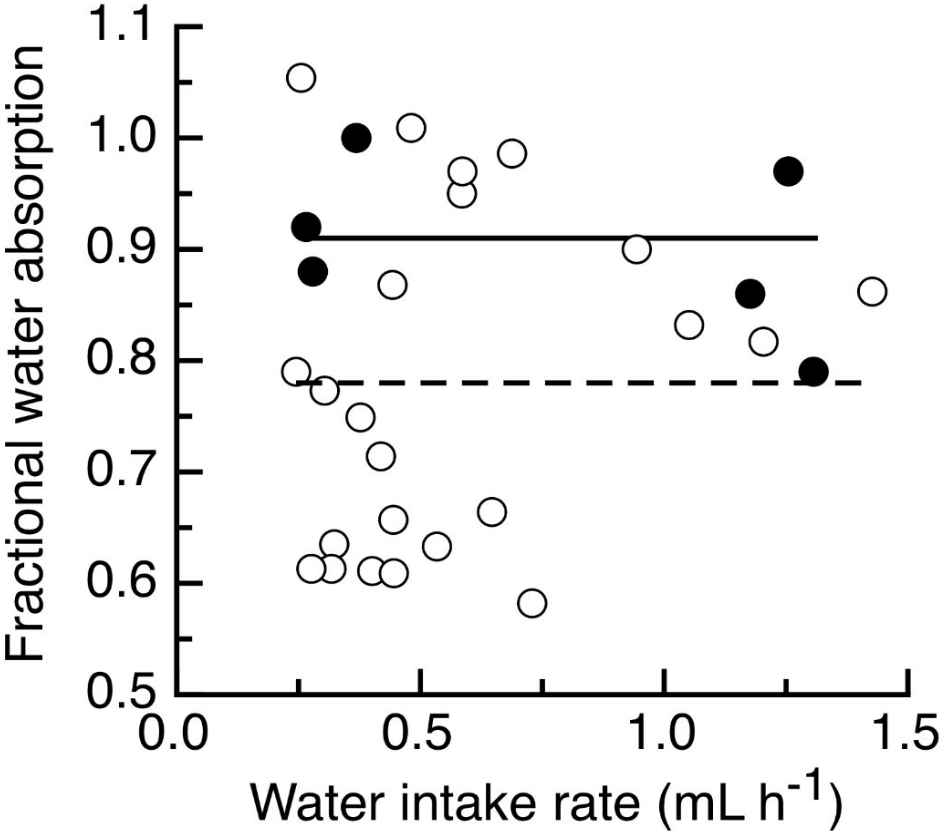

FIG. 1. In hummingbirds, water absorption in the intestinal tract is independent of water intake rate. Mean fractional water absorption in Green-backed Firecrowns (*Sephanoides sephanoides*; filled circles, solid line) and Broad-tailed Hummingbirds (*Selasphorus platycercus*; empty circles, broken line) was 0.91 (SD = 0.08, n = 6) and 0.78 (SD = 0.15, n = 23), respectively, across a broad range of water intake rates. These findings indicate that 1) hummingbirds do not regulate water absorption to avoid overhydration and 2) can experience large renal water loads. Data are from McWhorter & Martínez del Rio (1999) and Hartman Bakken & Sabat (2006).

birds has received scant attention (Nicolson 2006). Consequently, it is unclear if hummingbirds regulate insensible water losses in response to hydration status. In terms of avoiding overhydration, there is a positive relationship between evaporative water loss and water intake in hummingbirds (Lotz *et al.* 2003). Although such a relationship facilitates body water dissipation, the observed increase in total evaporative water loss appears to have resulted from increases in both metabolic rate and activity level (Withers 1992, Lotz *et al.* 2003) rather than a physiological or behavioral adjustment to eliminate body water.

DEHYDRATION AVOIDANCE

Renal water elimination requires different morphological characters and physiological

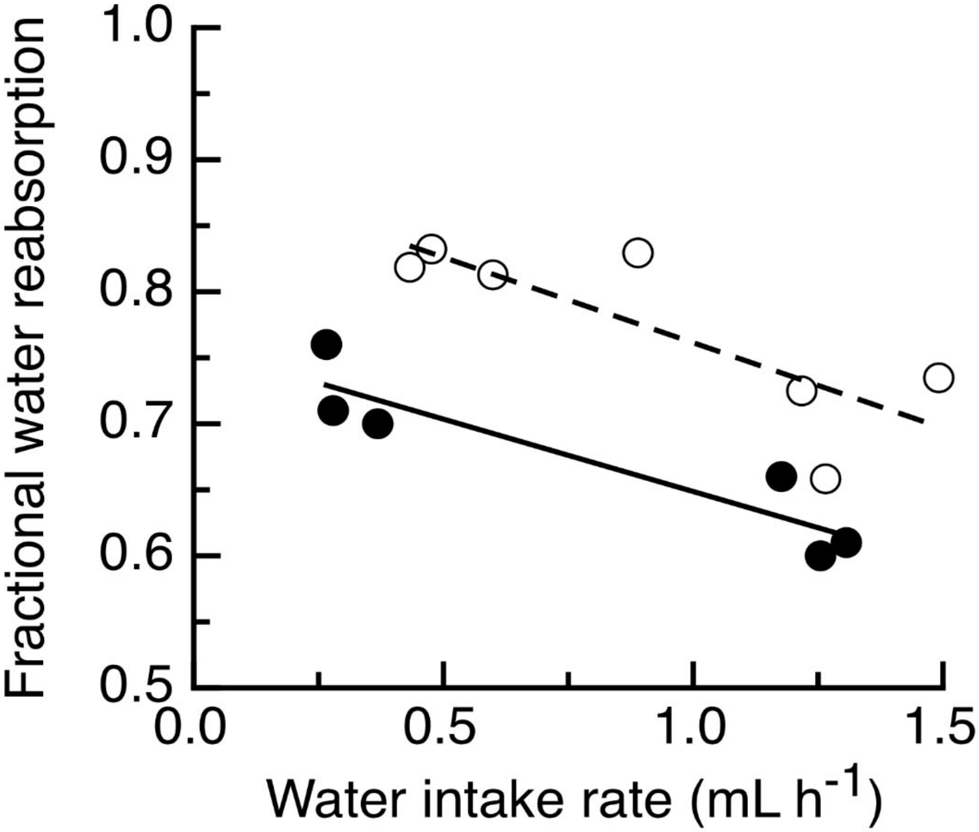

FIG. 2. Fractional water reabsorption in the kidney is responsive to water loading in hummingbirds. Both Green-backed Firecrowns (*Sephanoides sephanoides*; filled circles, solid line) and Broad-tailed Hummingbirds (*Selasphorus platycercus*; empty circles, broken line) reduce water reabsorption in the kidney as water intake rates increase. These relationships are described by the following linear functions for Green-backed firecrowns and Broad-tailed Hummingbirds, respectively: $y = 0.75 - 0.11x$ ($r^2 = 0.82$, $n = 6$) and $y = 0.89 - 0.13\,x$ ($r^2 = 0.66$, $n = 7$). Data are from Hartman Bakken *et al.* (2004) and Hartman Bakken & Sabat (2006).

processes than those necessary for renal water conservation (Danztler 1989). Consequently, the efficient elimination of excess ingested water by hummingbirds suggests their capacity to conserve body water during times of water stress is limited. For instance, the paucity of looped, mammalian-type nephrons in hummingbird kidneys (Casotti *et al.* 1998) precludes the formation of hyperosmotic urine (Lotz & Martínez del Rio 2004).

How then do hummingbirds avoid dehydration during fasting periods? Although GFR is only marginally responsive to water loading (Hartman Bakken *et al.* 2004), reducing GFR during times of water stress appears to be an essential water conserving strategy in hummingbirds (Fig. 3; Hartman Bakken *et al.* 2004, Hartman Bakken & Sabat 2006). For example, Broad-tailed Hummingbirds reduce GFR by ~50% when they are deprived of food (and thus water) for ~1.5 h. A reduction

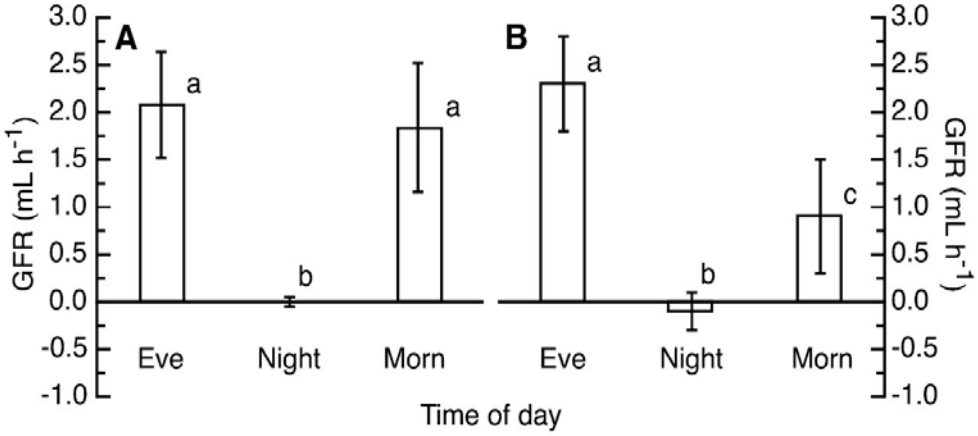

FIG. 3. Hummingbirds exhibit diel variation in glomerular filtration rate (GFR) and arrest whole-kidney GFR at night. (A) In Green-backed Firecrowns (*Sephanoides sephanoides*), GFRs were 2.08 ± 0.56, 0.00 ± 0.05, and 1.84 ± 0.68 mL h^{-1} (mean ± SD, n = 6) during the evening (eve), night, and morning (morn). (B) GFRs in Broad-tailed Hummingbirds (*Selasphorus platycercus*) show a similar pattern: during the eve, night, and morn, GFRs were 2.3 ± 0.5, – 0.1 ± 0.2, and 0.9 ± 0.6 mL h^{-1} (mean ± SD, n = 9). By ceasing renal filtration at night hummingbirds prevent body water losses to urine. Within each panel, the lowercase letters [a and b in panel (A); a, b, and c in panel (B)] denote statistically different GFRs. Data are from Hartman Bakken *et al.* (2004) and Hartman Bakken & Sabat (2006).

in GFR of this magnitude is typical for water-stressed birds; however, such a response is usually evident over the course of several days (Braun 1993). The sensitivity of GFR to dehydration is also evident during natural periods of fasting in hummingbirds. During the night, both the Broad-tailed Hummingbird and Green-backed Firecrown arrest whole-kidney GFR (Hartman Bakken *et al.* 2004, Hartman Bakken & Sabat 2006), a response that effectively prevents body water losses to urine (Fig. 3).

Despite reducing urinary water losses to zero at night (Fig. 3), the high mass-specific rates of total evaporative water loss in hummingbirds (Powers 1992, Williams 1996, and references there) appear to result in substantial body water losses (Hartman Bakken & Sabat 2007). Aside from a reduced metabolism during bouts of torpor (Powers 1991, López-Calleja & Bozinovic 1995), it is not clear if hummingbirds make adjustments to mitigate dehydration (Maloney & Dawson 1998, Hoffman & Walsberg 1999, Haugen *et al.* 2003a, 2003b; McKecknie & Wolf 2004). Indirect measurements, however, suggest they do not: during the night, Green-backed Firecrowns appear to lose ~25% of their total body water to evaporation (Hartman Bakken & Sabat 2007). The authors note, however, that this estimate is likely overstated. That is, the hyperphagic (and thus polydipsic) behavior of hummingbirds before lights-off in the evening (López-Calleja *et al.* 1997) means there will be a positive relationship between dietary water in nonabsorptive regions of the intestinal tract (i.e., crop) and the estimated proportion of total body water lost to evaporation during the night. Additionally, it is not known if and/or how body water volumes and osmolarities change during this period.

NECTAR SUGAR CONCENTRATION AND WATER BALANCE

Roughly thirty years ago, both Baker (1975) and Calder (1979) recognized that hummingbirds, even though they subsist on food that is watery, may experience water stress when feeding on nectar with high sugar concentrations. As hummingbirds will consume more than their body mass in water each day when feeding on nectar that is 25% (mass percent) sugar (Martínez del Rio *et al.* 2001), this hypothesis seems bewildering; however, there is experimental evidence to support it. To predict the maximum sugar concentration that hummingbirds can feed on and maintain water balance, data are needed on rates of 1) total evaporative water loss (μL H_2O h^{-1}) and 2) metabolism (mL O_2 h^{-1}; Calder 1979). For Green-backed Firecrowns, the total evaporative water loss rate to metabolic rate ratio is 1.49 ± 0.21 μL H_2O mL O_2^{-1} (mean ± SD, n = 8; Hartman Bakken & Sabat 2007). Applying this quotient to Calder's (1979) model suggests the highest sucrose concentration nectar that this species can maintain water balance on at 25°C is 620 mmol sucrose L^{-1} (or ~21%). This value is approximately the average sugar concentration of nectar produced by hummingbird-pollinated plants, although the range of sugar concentration is roughly 5–55% (Nicolson & Fleming 2003a, and references there). Interestingly, the work of Nicolson & Fleming (2003b), where White-bellied Sunbirds (*Nectarinia talatala*) drank increasing amounts of free water as the sugar concentration of their diet increased, suggests that the hypothesis forwarded by Baker (1975) and Calder (1979) is correct. In Bananaquits (*Coerba flaveola*), however, free water consumption was independent of nectar sugar concentration (Mata & Bosque 2004). A similar test has not been carried out in hummingbirds.

CONCLUSIONS AND A COMPARATIVE PERSPECTIVE

To date, studies concerned with water balance in hummingbirds suggest that they rely solely on their renal system to resolve the osmoregulatory quandary posed by their diet. Although less is known in other lineages of nectar-feeding birds, studies have revealed both evolutionary convergence and mechanistic diversity in the physiological processes that nectar-feeding birds use to maintain water balance. For example, both sunbirds (Nectariniidae) and honeyeaters (Meliphagidae) eliminate excess ingested water by reducing the fraction of filtered water reabsorbed in the kidney (Goldstein & Bradshaw 1998, McWhorter *et al.* 2004). Interestingly, sunbirds also appear to use the regulated water absorption mechanism hypothesized by Beuchat *et al.* (1990) to avoid overhydrating (McWhorter *et al.* 2003). Unfortunately, no data are available for nectar-feeding mammals and dehydration avoidance has only been studied in hummingbirds. As other lineages are studied, however, the gradients of nectarivory (Pyke 1980, Carthew & Goldingay 1997), mass, and renal morphology (Casotti & Richardson 1992, Casotti *et al.* 1998, Schondube *et al.* 2001) among nectar-feeding vertebrates will elucidate the influence diet, body size, and phylogeny exert on the processes they use to maintain water balance.

ACKNOWLEDGMENTS

We thank Todd J. McWhorter for making the Broad-tailed Hummingbird data in Figure 1 available and Carlos Martínez del Rio for criticizing an earlier draft of this article. BHB's participation in the VIIIth Neotropical Ornithological Congress and this symposium was, in part, funded by the University of Wyoming's College of Arts and Sciences, Department of Zoology and Physiology, and Graduate School.

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