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DO NECTAR- AND FRUIT-EATING BIRDS HAVE LOWER NITROGEN REQUIREMENTS THAN OMNIVORES? AN ALLOMETRIC TEST

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ABSTRACT.—We used an allometric approach to compare the minimum nitrogen requirements (MNR) and the total endogenous nitrogen loss (TENL) of nectar- and fruit-eating birds with those of omnivorous birds. These two parameters were 4× higher in omnivores than in nectarivores and frugivores. In nectarivorous–frugivorous birds, MNR was 152.8 mg N kg^{-0.76} day⁻¹; in omnivorous birds, it was 575.4 mg N kg^{-0.76} day⁻¹. Similarly, TENL was 54.1 mg N kg^{-0.69} day⁻¹ in nectarivores–frugivores, and 215.3 mg N kg^{-0.69} day⁻¹ in omnivores. The residuals of the allometric relationships between TENL and MNR and body mass were positively correlated, which suggests that a large proportion of the interspecific variation in MNR is explained by variation in TENL. Although our results show that nectar- and fruit-eating birds have low nitrogen requirements, the mechanisms that these animals use to conserve nitrogen remain unclear. *Received 23 August 2005, accepted 8 November 2005.*

Key words: allometry, frugivorous birds, minimum nitrogen requirements, nectarivorous birds, omnivorous birds, phylogeny, total endogenous nitrogen loss.

Do Nectar- and Fruit-eating Birds Have Lower Nitrogen Requirements than Omnivores? An Allometric Test

RESUMEN.—We used an allometric approach to compare the minimum nitrogen requirements (MNR) and the total endogenous nitrogen loss (TENL) of nectar- and fruit-eating birds with those of omnivorous birds. These two parameters were 4× higher in omnivores than in nectarivores and frugivores. In nectarivorous–frugivorous birds, MNR was 152.8 mg N kg^{-0.76} day⁻¹; in omnivorous birds, it was 575.4 mg N kg^{-0.76} day⁻¹. Similarly, TENL was 54.1 mg N kg^{-0.69} day⁻¹ in nectarivores–frugivores, and 215.3 mg N kg^{-0.69} day⁻¹ in omnivores. The residuals of the allometric relationships between TENL and MNR and body mass were positively correlated, which suggests that a large proportion of the interspecific variation in MNR is explained by variation in TENL. Although our results show that nectar- and fruit-eating birds have low nitrogen requirements, the mechanisms that these animals use to conserve nitrogen remain unclear.

NITROGEN CAN BE a limiting resource for animals (Mattson 1980, White 1993, Witmer 1998), which require it in the form of essential and nonessential amino acids and for the synthesis

of other nitrogenous compounds (Klasing 1998). White (1993) provides a large number of examples of animal populations that are limited not by the availability of energy, but by the scarcity of nitrogen. However, not all animals experience nitrogen limitation to the same extent. The amount and quality of protein varies among

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diets (Klasing 1998, Pryor 2003). It is widely believed that the nitrogen needs of animals match their diets' protein content (Witmer 1998, Bosque and Pacheco 2000). Nectar and fruit pulp, for example, contain very low levels of protein (Brice and Grau 1991, Izhaki 1993, Witmer 1998, Gartrell 2000), and several authors have hypothesized that animals that feed on them have low nitrogen requirements (Bosque and Pacheco 2000, Roxburgh and Pinshow 2000, van Tets and Nicolson 2000, McWhorter et al. 2003).

Nitrogen requirements are traditionally estimated by two parameters: minimum nitrogen requirements (MNR) and total endogenous nitrogen loss (TENL). The latter estimates the nitrogen losses on nitrogen-free diets, whereas the former estimates the amount of nitrogen required to achieve nitrogen balance (i.e., intake equals excretion). Minimum nitrogen requirements and TENL are useful comparative tools that estimate the nitrogen requirements of animals that are not growing and that are nonreproductive (Klasing 1998). The most widely used method to measure MNR and TENL is to feed birds diets that share the same ingredients and differ only in their protein content. Typically, nitrogen balance (the difference between nitrogen intake and total excreted nitrogen) and intake are related by a linear function. Thus, TENL is estimated as the y -intercept of this function, which represents the nitrogen losses when the animal is ingesting no protein. Minimum nitrogen requirement is estimated by calculating the x -intercept of this function, when presumably animals are in nitrogen balance and ingest as much nitrogen as they lose (Brice and Grau 1991, Korine et al. 1996, Witmer 1998, Allen and Hume 2001, Roxburgh and Pinshow 2000, Pryor et al. 2001).

Both MNR and TENL are functions of body mass. Robbins (1993) found that the scaling exponent of these allometric relationships was ~ 0.75 and established two predictive relationships that are widely used. He estimated that MNR and TENL equal $430 \text{ mg N kg}^{-0.75} \text{ day}^{-1}$ and $270 \text{ mg N kg}^{-0.75} \text{ day}^{-1}$, respectively. To examine whether Robbins's (1993) estimates apply to nectarivorous and frugivorous birds and to test the hypothesis that the N requirements of these animals are lower than those of omnivores, we compiled and analyzed available data on the MNR and TENL of various avian species. The data in our analyses originated from studies that satisfied two criteria: (1) the studied birds were not growing

or reproductive, and (2) the study was designed to explicitly measure MNR and TENL (Table 1). In addition to conducting a standard regression analysis, we compared the nitrogen requirements of nectarivorous and frugivorous birds with those of omnivores using a qualitative, but phylogenetically explicit, comparison. Our results verified that MNR and TENL both scale with body mass to the 0.75 power and confirmed the hypothesis that nectarivorous and frugivorous birds have relatively low nitrogen requirements.

METHODS

Because MNR and TENL are related to body mass by a power function, we log-transformed all data before analysis. We used a linear model to assess whether the relationship between log body mass and log MNR and log TENL differed between nectarivores and frugivores. We found that these relationships did not differ in either intercept (MNR: $F = 0.004$, $df = 1$ and 10 ; TENL: $F = 0.0068$, $df = 1$ and 10 ; $P > 0.5$) or slope (MNR: $F = 0.53$, $df = 1$ and 10 ; TENL: $F = 2.4$, $df = 1$ and 10 ; $P > 0.2$). Thus, we pooled nectarivorous and frugivorous birds into a single category. Our phylogenetic comparison was based on Sibley and Ahlquist's (1991) DNA-DNA hybridization phylogenetic hypothesis. Because the number of species in our analysis was small and taxonomically biased (Table 1), a proper phylogenetic analysis, such as phylogenetically independent contrasts (Felsenstein 1985, Garland and Ives 2000), was impossible. Our sample is taxonomically biased (e.g., 6 of the 11 species of nectar-feeding birds are hummingbirds) and, thus, the traits in question are clumped within the phylogeny. Under these conditions, available phylogenetic methods have low power (see Schondube et al. 2001). Thus, we conducted only a qualitative, phylogenetically informed comparison. The purpose of this comparison was to assess whether nectarivorous-frugivorous birds have lower TENL and MNR than the most closely related clades for which information is available. A proper statistical analysis that includes phylogeny must await a more evenly distributed sampling of taxa.

STATISTICS

We used a linear model to compare the relations of (1) log body mass to log MNR and (2) log TENL of nectarivorous-frugivorous birds

TABLE 1. Body mass, minimum nitrogen requirements (MNR), and total endogenous nitrogen loss (TENL) of the reviewed species.

Species	Scientific name	Body mass (g)	MNR (mg N day ⁻¹)	TENL (mg N day ⁻¹)	Source
Nectarivores					
Red Lory	<i>Eos bornea</i>	163.00	33.30	25.60	Pryor 2003
Rainbow Lorikeet	<i>Trichoglossus haematodus</i>	151.00	58.59	7.85	Frankel and Avram 2001
New Holland Honeyeater	<i>Phylidonyris novaehollandiae</i>	20.00	4.90	3.20	Paton 1982
Lesser Double-collared Sunbird	<i>Nectarinia chalybea</i>	8.00	6.80	4.20	van Tets and Nicolson 2000
Blue-throated Hummingbird	<i>Lampornis clemenciae</i>	7.90	3.24	1.69	McWhorter et al. 2003
Magnificent hummingbird	<i>Eugenes fulgens</i>	7.50	4.03	1.98	McWhorter et al. 2003
Orange-tufted Sunbird	<i>Nectarinia osea</i>	6.90	5.10	1.90	Roxburgh and Pinshow 2000
Green-backed Firecrown	<i>Sephanoides sephanioides</i>	6.22	1.42	1.33	Lopez-Calleja et al. 2003
Costa's Hummingbird	<i>Calypte costae</i>	3.80	4.50	1.12	Brice and Grau 1991
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	3.40	0.88	0.64	McWhorter 1997
Black-chinned Hummingbird	<i>Archilochus alexandri</i>	2.70	1.01	0.54	McWhorter et al. 2003
Frugivores					
Pesquet's Parrot	<i>Psittrichas fulgidus</i>	757.00	259.70	40.58	Pryor et al. 2001
Tristram's Grackle	<i>Onychognathus tristrami</i>	115.00	24.70	19.90	Tsahar et al. 2005b
Yellow-vented Bulbul	<i>Pycnonotus xanthopygos</i>	36.00	8.16	6.20	Tsahar et al. 2005b
Cedar Waxwing	<i>Bombycilla cedrorum</i>	34.50	21.20	5.50	Witmer 1998
Omnivores					
Wild Turkey	<i>Meleagris gallopavo</i>	8,290.00	2,130.53	704.65	Moran et al. 1983
Chicken	<i>Gallus gallus domesticus</i>	2,500.00	700.00	357.60	Leveille and Fisher 1958
Magpie Goose	<i>Anseranas semipalmata</i>	2,190.00	936.13	–	Dawson et al. 2000
European Starling	<i>Sturnus vulgaris</i>	72.00	81.10	44.30	Tsahar et al. 2005a
American Robin	<i>Turdus migratorius</i>	65.70	62.80	25.50	Witmer 1998
Wood Thrush	<i>Hylocichla mustelina</i>	47.10	92.10	26.10	Witmer 1998
Budgerigar	<i>Melopsittacus undulatus</i>	42.00	35.30	24.10	Pryor 2003
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	27.70	58.56	14.60	Murphy 1993
House Sparrow	<i>Passer domesticus</i>	26.95	75.90	58.79	Weglarczyk 1981
Zebra Finch	<i>Taeniopygia guttata</i>	11.79	14.42	5.47	Allen and Hume 2001

to that of omnivorous birds. The linear model used in the analysis was $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \varepsilon$, where y is the dependent variable (log of either MNR or TENL), x_1 is log body mass, x_2 is a dummy variable that represents the effect of guild (omnivore vs. nectarivore–frugivore), β_0 the intercept for omnivores, β_1 the slope for omnivores, β_2 the difference between the intercepts of the guilds and β_3 the difference between their slopes. If β_3 was not statistically different from zero, we dropped this interaction term from the analysis and calculated a reduced model. To test whether TENL and MNR are related, we correlated the residuals of the log–log relationships between these measurements and body mass. Data are reported as means \pm SE. Scientific names of all species reviewed are given in Table 1.

RESULTS

Both MNR and TENL increased as a function of body mass (Fig. 1). Log MNR was closely and linearly related to log body mass ($F = 224.94$, $df = 1$ and 21 , $P < 0.001$). We found a significant difference in the intercept of the relationship between log body mass and log MNR between omnivorous and nectarivorous–frugivorous birds ($F = 36.11$, $df = 1$ and 21 , $P < 0.001$). However, we found no significant differences in the slope ($F = 3.30$, $df = 1$ and 21 , $P > 0.10$). Therefore, we eliminated the interaction term of the model and recalculated a common slope. We found that its value equaled 0.76 ± 0.06 (Fig. 1). Similarly, we found that the relationship between log body mass and log TENL was linear ($F = 189.88$, $df = 1$ and 21 , $P < 0.001$) and that the intercept of this relationship differed significantly between omnivores and nectarivores–frugivores ($F = 44.99$, $df = 1$ and 21 , $P < 0.001$). We also found that the slopes of this relationship did not differ between these two groups ($F = 0.74$, $df = 1$ and 21 , $P > 0.20$). After the interaction term was removed, the common slope equaled 0.69 ± 0.05 (Fig. 1), which is not significantly different from 0.75 ($t = 1.2$, $P > 0.3$). Minimum nitrogen requirements and TENL were $\sim 4\times$ higher in omnivorous than in nectarivorous–frugivorous birds. The residuals of the allometric relationships between TENL and MNR and body mass were positively and linearly related ($F = 33.86$, $df = 1$ and 22 , $P < 0.0001$; Fig. 2). This relationship suggests that

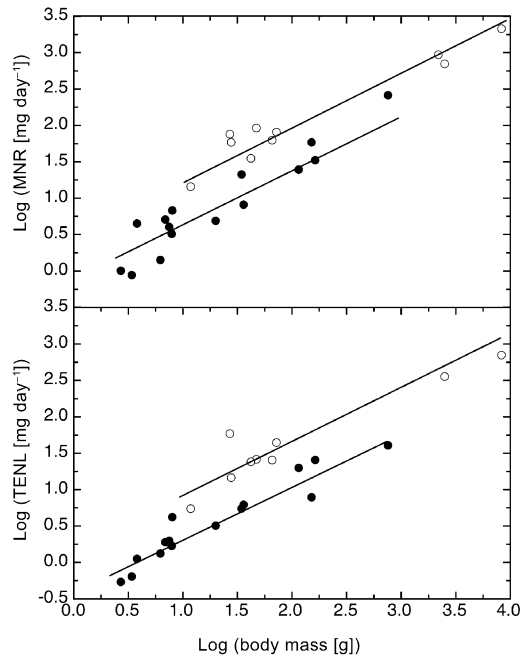


FIG. 1. Both minimum nitrogen requirements (MNR; upper panel) and total endogenous nitrogen loss (TENL; lower panel) increase as a function of body mass, and both are $\sim 4\times$ higher in omnivores (empty circles; $\log\text{MNR} = 0.48 + 0.76\log\text{BM}$, $\log\text{TENL} = 0.26 + 0.69\log\text{BM}$) than in nectarivores–frugivores (filled circles; $\log\text{MNR} = -0.096 + 0.76\log\text{BM}$, $\log\text{TENL} = -0.34 + 0.69\log\text{BM}$).

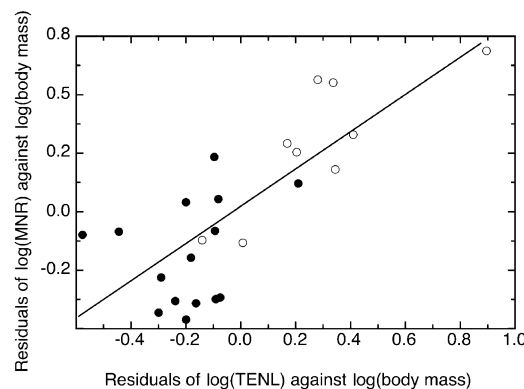


FIG. 2. Residuals of the allometric relationships between TENL and MNR on body mass are positively related ($y = 0.800x - 0.002$, $r^2 = 0.61$, $P < 0.0001$; empty circles = omnivores, filled circles = nectarivores–frugivores).

the MNR increases with TENL when both parameters are standardized for body mass. The phylogenetic tree in Figure 3 illustrates that, in all cases, the MNR of the frugivorous and the nectarivorous clades were lower than that of the most closely related omnivorous species.

DISCUSSION

Nitrogen requirements of nectarivorous and frugivorous birds, as estimated by MNR and

TENL, seem to be ~25% that of omnivorous birds. Although the allometric relationships between MNR and TENL and body mass differ between these two groups, the exponents of these relationships are similar and do not differ from 0.75. Our estimates for omnivores are only slightly different from Robbins's (1993) values (Table 2). The large differences in TENL and MNR between omnivores and nectarivores–frugivores emphasize the need to recognize that specialization on different diets is accompanied by differences in

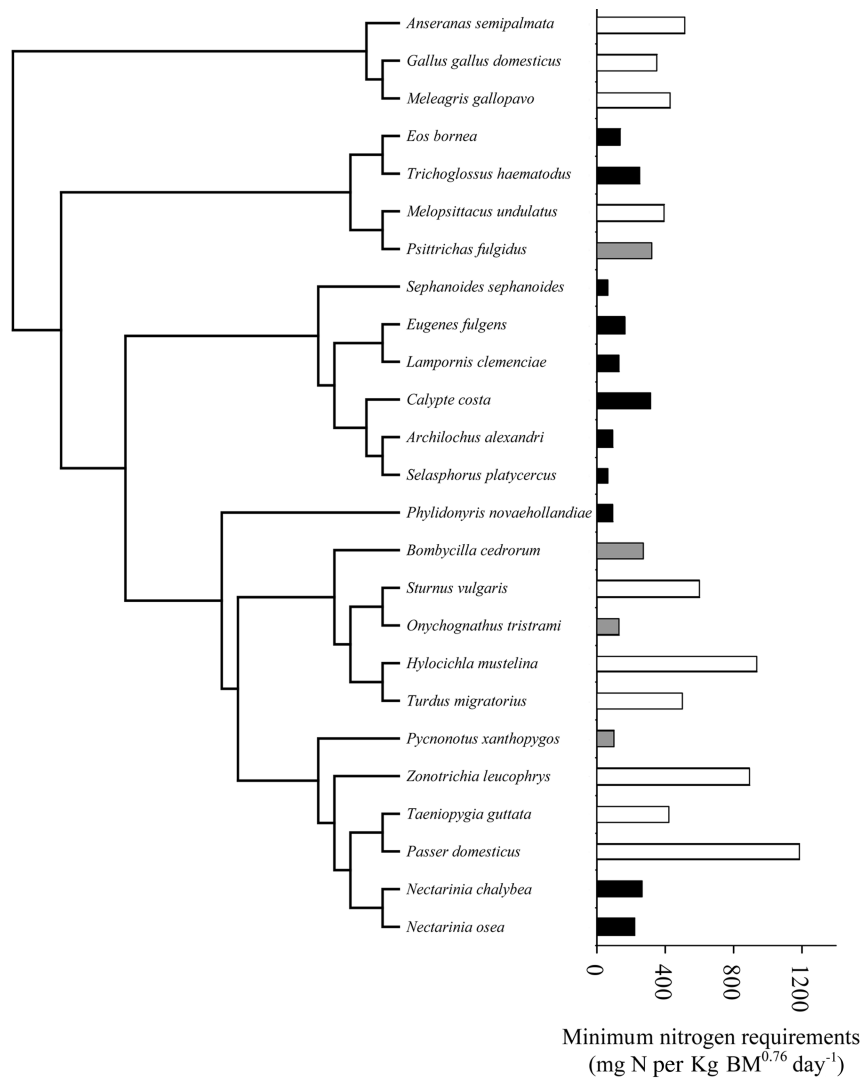


FIG. 3. Mass-specific nitrogen requirements of nectar-eating birds (black bars) and fruit-eating birds (gray bars) are lower than those of omnivorous species (white bars) in the most closely related clades for which data are available.

TABLE 2. Minimal nitrogen requirements (MNR) and total endogenous nitrogen losses (TENL) of nectar- and fruit-eating birds are lower than those of omnivores. The allometric values estimated with a larger species sample of omnivores are slightly different from those estimated by Robbins (1993). Robbins (1993) estimated TENL and MNR as 270 and 430 mg kg^{-0.75} day⁻¹, respectively.

	TENL (mg kg ^{-0.69} day ⁻¹)	MNR (mg kg ^{-0.76} day ⁻¹)
Nectarivores–frugivores	54.1	152.8
Omnivores	215.3	575.4

nitrogen requirements. Although our phylogenetic comparison is based on a limited number of clade comparisons, it supports the notion that nectarivorous–frugivorous birds have lower nitrogen requirements than omnivorous birds. It also suggests, albeit tentatively, that low nitrogen requirements evolved concurrently with the habit of feeding on nectar or fruit and, hence, with the need to cope with low-protein diets.

Although the ultimate evolutionary causes for the low nitrogen requirements of nectarivorous–frugivorous birds appear to be clear, the proximate physiological mechanisms that allow these animals to subsist on low-protein diets are neither fully understood nor well studied. A possibility is that the low nitrogen requirements of nectarivorous–frugivorous birds are not the result of their physiological traits but a direct consequence of the characteristics of their diets. The positive relationship between MNR and TENL illustrated in Figure 2 suggests that a large proportion of the interspecific variation in MNR is explained by variation in TENL. There are two components of TENL: endogenous urinary nitrogen losses (EUNL) and metabolic fecal nitrogen (MFN) (Robbins 1993). Nectar and fruit are characterized by low contents of protein, lipids, and fibers. Hence, assimilating their nutrients does not require the secretion of pancreatic enzymes and bile acids (Bosque and Pacheco 2000). These products contain most of the nitrogen lost as MFN (Robbins 1993). Thus, one possible explanation for the low nitrogen requirements of nectarivorous–frugivorous birds is that their diets reduce the loss of metabolic fecal nitrogen (MFN).

Indeed, low MFN losses seem to be prevalent among nectar- and fruit-eating vertebrates. Delorme and Thomas (1996, 1999) found low MFN losses in fruit bats (*Carollia perspicillata*, *Artibeus jamaicensis*, and *Rousettus aegyptiacus*), and Smith and Green (1987) found low values in sugar gliders (*Petaurus breviceps*). McWhorter et al. (2003) reported that 95% of all the nitrogen excreted by hummingbirds was in the form of urinary nitrogen (urate, ammonia, urea, and creatinine). To test whether the *per se* was a determinant of nitrogen requirements, Tsahar et al. (2005a) measured the nitrogen requirements of the omnivorous European Starling, fed on nectar-like diets (water, sugars, and a low level of protein). They found that the MNR and TENL of these birds were indistinguishable from those expected for an omnivorous species. They also found that, as with hummingbirds, urinary nitrogen, rather than fecal nitrogen, was the major vehicle of nitrogen losses in European Starlings. They concluded that a nectar-like fluid diet, by itself, does not significantly decrease the nitrogen requirements of omnivores. Although nectar and fruit diets can contribute to the low nitrogen requirements of nectarivores and frugivores, they cannot fully explain them.

The observation that metabolic fecal nitrogen represents only a small fraction of the total endogenous nitrogen losses in nectarivorous–frugivorous birds points to urinary nitrogen loss as the primary determinant of their nitrogen requirements. Why should nectarivorous–frugivorous birds have low endogenous urinary nitrogen losses? Factors that can decrease EUNL include low rates of protein turnover, high rates of metabolic nitrogen recycling, and a high capacity for digestive nitrogen recycling (Witmer 1998, Pryor et al. 2001). We make a distinction between metabolic and digestive recycling to recognize that each of these processes is explained by different physiological mechanisms. By “metabolic recycling,” we refer to the reuse of nitrogen derived from the catabolism of amino acids to synthesize dispensable amino acids (see Carleton and Martínez del Río 2005). Protein turnover and metabolic nitrogen recycling have not been investigated from a comparative perspective in nectarivorous–frugivorous birds. They remain potentially important mechanisms that can explain the low nitrogen requirements of these animals.

Digestive N recycling involves the breakdown of urinary N (urate, urea, or both) by microorganisms that thrive in the gastrointestinal tract, followed by either absorption of liberated ammonia or assimilation of protein synthesized by these microorganisms (Karasawa et al. 1988, Karasawa and Maeda 1995, Karasawa 1999). Preest et al. (2003) reported bacteria with uricase activity in the gastrointestinal tract of Anna's Hummingbirds (*Calypte anna*), and Roxburgh and Pinshow (2002) and Tsahar et al. (2005b) found postrenal urine modification in the nectarivorous Orange-tufted Sunbird and in the frugivorous Yellow-vented Bulbul, respectively. In both of these species, when birds ingested diets with a high water content and a low protein content, the proportion of nitrogen excreted as urate decreased and that of ammonia increased in excreta but not in ureteral urine. Tsahar et al. (2005b) speculated that post-renal urine modification could result from bacterial degradation. Although these observations are suggestive of digestive nitrogen recycling in nectarivorous–frugivorous birds, they do not constitute proof of its quantitative importance.

Digestive recycling by bacteria is physiologically important in avian species with large cecae and, hence, with a well-developed gastrointestinal microbiota (Mortensen and Tindall 1981; Campbell and Braun 1986; Karasawa et al. 1988, 1993; Son and Karasawa 2000). However, most nectarivorous–frugivorous birds have only vestigial cecae. Hummingbirds, arguably the most specialized avian nectarivores, have no cecae (Clench 1999). Therefore, it seems that the gastrointestinal tracts of birds that feed on fruit or nectar do not have the structures needed to house the large microbiota presumably required for effective digestive nitrogen recycling. The contribution of bacteria to the nitrogen balance of nectarivorous–frugivorous birds remains to be demonstrated.

Another mechanism that may contribute to digestive nitrogen recycling is the reabsorption of amino acids from the lower gut. Many bird species propel ureteral urine aborally and, thus, place it in contact with the epithelial surface of the hindgut, which can express significant levels of membrane-bound peptidases (Witmer and Martínez del Río [2001] and references therein). Uric acid in birds is excreted as a component of spheres that also contain protein and inorganic ions (Casotti and Braun 1997, Goldstein and

Skadhauge 2000). It may be that nectar- and fruit-eating birds are capable of assimilating the protein within these spheres. This mechanism may explain post-renal urine modification found in the frugivorous Yellow-vented Bulbul, in which concentration of protein was 3× higher in ureteral urine than in excreta (Tsahar et al. 2005b). The long microvilli found in the lower gut of Pesquet's Parrots (Guntert 1981, as cited in Pryor et al. 2001), and other nectar- and fruit-eating birds (Witmer and Martínez del Río 2001), could enhance the recovery of excreted protein.

In summary, although our results support the notion that nectarivorous–frugivorous birds have low nitrogen requirements, we cannot yet offer an adequate mechanistic explanation for why these requirements are as low as they are. We hypothesize that a combination of low protein turnover and high metabolic nitrogen recycling explain why avian nectarivores and frugivores can rely on their remarkably protein-poor diets.

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LITERATURE CITED

- ALLEN, L. R., AND I. D. HUME. 2001. The maintenance nitrogen requirements of the Zebra Finch *Taeniopygia guttata*. *Physiological and Biochemical Zoology* 74:366–375.
- BOSQUE, C., AND M. A. PACHECO. 2000. Dietary nitrogen as a limiting nutrient in frugivorous birds. *Revista Chilena de Historia Natural* 73:441–450.
- BRICE, A. T., AND C. R. GRAU. 1991. Protein requirements of Costa's Hummingbirds *Calypte costae*. *Physiological Zoology* 64: 611–626.
- CAMPBELL, C. E., AND E. J. BRAUN. 1986. Cecal degradation of uric acid in Gambel quail. *American Journal of Physiology* 251: R59–R62.
- CARLETON, S. A., AND C. MARTÍNEZ DEL RÍO. 2005. The effect of cold-induced increased

- metabolic rate on the rate of ^{13}C and ^{15}N incorporation in House Sparrows (*Passer domesticus*). *Oecologia* 144:226–232.
- CASOTTI, G., AND E. J. BRAUN. 1997. Ionic composition of urate-containing spheres in the urine of domestic fowl. *Comparative Biochemistry and Physiology* 118A:585–588.
- CLENCH, M. H. 1999. The avian cecum: Update and motility review. *Journal of Experimental Zoology* 283:441–447.
- DAWSON, T. J., P. J. WHITEHEAD, A. McLEAN, F. D. FANNING, AND W. R. DAWSON. 2000. Digestive function in Australian Magpie Geese (*Anseranas semipalmata*). *Australian Journal of Zoology* 48:265–279.
- DELORME, M., AND D. W. THOMAS. 1996. Nitrogen and energy requirements of the short-tailed fruit bat (*Carollia perspicillata*): Fruit bats are not nitrogen constrained. *Journal of Comparative Physiology B* 166:427–434.
- DELORME, M., AND D. W. THOMAS. 1999. Comparative analysis of the digestive efficiency and nitrogen and energy requirements of the phyllostomid fruit-bat (*Artibeus jamaicensis*) and the pteropodid fruit-bat (*Rousettus aegyptiacus*). *Journal of Comparative Physiology B* 169:123–132.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783–791.
- FRANKEL, T. L., AND D. AVRAM. 2001. Protein requirements of Rainbow Lorikeets, *Trichoglossus haematodus*. *Australian Journal of Zoology* 49:435–443.
- GARLAND, T., JR., AND A. R. IVES. 2000. Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* 155:346–364.
- GARTRELL, B. D. 2000. The nutritional, morphologic, and physiologic bases of nectarivory in Australian birds. *Journal of Avian Medicine and Surgery* 14:85–94.
- GOLDSTEIN, D. L., AND E. SKADHAUGE. 2000. Renal and extrarenal regulation of body fluid composition. Pages 265–297 in *Sturkie's Avian Physiology*, 5th ed. (G. C. Whittow, Ed.). Academic Press, San Diego, California.
- GUNTERT, M. 1981. Morphologische Untersuchungen zur adaptiven Radiation des Verdauungstraktes bei Papageien (Psittaci). *Zoologisches Jahrbuch der Anatomie* 106:471–526.
- IZHAKI, I. 1993. Influence of nonprotein nitrogen on estimation of protein from total nitrogen in fleshy fruits. *Journal of Chemical Ecology* 19:2605–2615.
- KARASAWA, Y. 1999. Significant role of the nitrogen recycling system through the ceca occurs in protein-depleted chickens. *Journal of Experimental Zoology* 283:418–425.
- KARASAWA, Y., T. ONO, AND H. KAWAI. 1988. Ammonia production from uric acid and its absorption from the caecum of the cockerel. *British Poultry Science* 29:119–124.
- KARASAWA, Y., T. ONO, AND K. KOH. 1993. Relationship of decreased caecal urease activity by dietary penicillin to nitrogen utilization in chicken fed on a low protein diet plus urea. *British Poultry Science* 35:91–96.
- KARASAWA, Y., AND M. MAEDA. 1995. *In situ* degradation and absorption of (^{15}N) urea in chicken ceca. *Comparative Biochemistry and Physiology* 111A:223–227.
- KLASING, K. C. 1998. *Comparative Avian Nutrition*. CAB International, Wallingford, United Kingdom.
- KORINE, C., Z. ARAD, AND A. ARIELI. 1996. Nitrogen and energy balance of the fruit bat *Rousettus aegyptiacus* on natural fruit diets. *Physiological Zoology* 69:618–634.
- LEVEILLE, G. A., AND H. FISHER. 1958. The amino acid requirements for maintenance in the adult rooster. I. Nitrogen and energy requirements in normal and protein-depleted animals receiving whole egg protein and amino acid diets. *Journal of Nutrition* 66:441–453.
- LOPEZ-CALLEJA, M. V., M. J. FERNÁNDEZ, AND F. BOZINOVIC. 2003. The integration of energy and nitrogen balance in the hummingbird *Sephanoides sephaniodes*. *Journal of Experimental Biology* 206:3349–3359.
- MATTSON, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119–161.
- McWHORTER, T. J. 1997. Energy assimilation, protein balance, and water absorption in Broad-tailed Hummingbirds, *Selasphorus platycercus*. M.S. thesis, University of Wyoming, Laramie.
- McWHORTER, T. J., D. R. POWERS, AND C. MARTÍNEZ DEL RIO. 2003. Are hummingbirds facultatively ammonotelic? Nitrogen excretion and requirements as a function of body size. *Physiological and Biochemical Zoology* 76:731–743.

- MORAN, E. T., P. R. FERKET, AND J. R. BLACKMAN. 1983. Maintenance nitrogen requirement of the turkey breeder hen with an estimate of associated essential amino acid needs. *Poultry Science* 62:1823–1829.
- MORTENSEN, A., AND A. R. TINDALL. 1981. Caecal decomposition of uric acid in captive and free ranging Willow Ptarmigan (*Lagopus lagopus lagopus*). *Acta Physiologica Scandinavica* 111:129–133.
- MURPHY, M. E. 1993. The protein requirement for maintenance in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. *Canadian Journal of Zoology* 71:2111–2120.
- PATON, D. C. 1982. The diet of the New Holland Honeyeater, *Phylidonyris novaehollandiae*. *Australian Journal of Ecology* 7:279–298.
- PREEST, M. R., D. G. FOLK, AND C. A. BEUCHAT. 2003. Decomposition of nitrogenous compounds by intestinal bacteria in hummingbirds. *Auk* 120:1091–1101.
- PRYOR, G. S. 2003. Protein requirements of three species of parrots with distinct dietary specializations. *Zoo Biology* 22:163–177.
- PRYOR, G. S., D. J. LEVEY, AND E. S. DIERENFELD. 2001. Protein requirements of a specialized frugivore, Pesquet's Parrot (*Psittichas fulgidus*). *Auk* 118:1080–1088.
- ROBBINS, C. T. 1993. *Wildlife Feeding and Nutrition*, 2nd ed. Academic Press, San Diego, California.
- ROXBURGH, L., AND B. PINSHOW. 2000. Nitrogen requirements of an Old World nectarivore, the Orange-tufted Sunbird *Nectarinia osea*. *Physiological and Biochemical Zoology* 73: 638–645.
- ROXBURGH, L., AND B. PINSHOW. 2002. Ammonotelic in a passerine nectarivore: The influence of renal and post-renal modification on nitrogenous waste product excretion. *Journal of Experimental Biology* 205:1735–1745.
- SCHONDUBE, J., C. MARTÍNEZ DEL RIO, AND L. G. HERRERA. 2001. Diet and the evolution of digestion and renal function in phyllostomid bats. *Zoology* 104:59–74.
- SIBLEY, C. G., AND J. E. AHLQUIST. 1991. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven, Connecticut.
- SMITH, A. P., AND S. W. GREEN. 1987. Nitrogen requirements of the sugar glider (*Petaurus breviceps*), an omnivorous marsupial, on a honey-pollen diet. *Physiological Zoology* 60:82–92.
- SON, J. H., AND Y. KARASAWA. 2000. Effect of removal of caecal content on nitrogen utilization and nitrogen excretion in caecally ligated chickens fed on a low protein diet supplemented with urea. *British Poultry Science* 41:69–71.
- TSAHAR, E., C. MARTÍNEZ DEL RIO, Z. ARAD, J. P. JOY, AND I. IZHAKI. 2005a. Are the low protein requirements of nectarivorous birds the consequence of their sugary and watery diet? A test with an omnivore. *Physiological and Biochemical Zoology* 78:239–245.
- TSAHAR, E., C. MARTÍNEZ DEL RIO, I. IZHAKI, AND Z. ARAD. 2005b. Can birds be ammonotelic? Nitrogen balance and excretion in two frugivores. *Journal of Experimental Biology* 208: 1025–1034.
- VAN TETS, I. G., AND S. W. NICOLSON. 2000. Pollen and the nitrogen requirements of the Lesser Double-collared Sunbird. *Auk* 117:826–830.
- WEGLARCYK, G. 1981. Nitrogen balance and energy efficiency of protein deposition of the House Sparrow. *Ekologia Polska* 29: 519–533.
- WHITE, T. C. R. 1993. *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer-Verlag, New York.
- WITMER, M. C. 1998. Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. *Physiological Zoology* 71: 599–610.
- WITMER, M. C., AND C. MARTÍNEZ DEL RIO. 2001. The intestinal enzymes of Cedar Waxwings and thrushes. *Physiological and Biochemical Zoology* 74:584–593.