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NITROGEN EXCRETION BY TURKEY VULTURES

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ABSTRACT.—The proportions of nitrogen (N), as urate-N (76.1%), NH_3-N (16.4%), and urea-N (7.5%) in the urine of fasted Turkey Vultures, are similar to those found in the urine of domestic chickens and ducks, the only other birds for which comparable data are available. Vultures show an adaptive increase in the percentage of urinary N excreted as urate (up to 86.8%) and a decrease in NH_3-N (down to 8.9%) and urea-N (down to 4.3%) in the period after feeding on meat. These alterations in the proportions of nitrogenous wastes increase the efficiency of N excretion; fed birds excrete 4.8 times more N per milliliter of urinary water than fasted birds. The efficiency of N excretion during the 1.5-h period after feeding is comparable to that of the most efficient mammalian excretory systems.

The elimination of urate (i.e., uric acid or any other urate compound) as the major nitrogenous excretory compound of birds generally is considered to be an adaptation for water conservation. Needham (1938) described the benefits of urate as a nitrogenous end product in cleidoic eggs; the potential osmotic advantage of urate excretion to adult birds is discussed in most current avian physiology texts (e.g., Sykes 1971, Shoemaker 1972, Sturkie 1976). The low solubility of urate in water (Peters and van Slyke 1946) and its ability to form colloids (Young and Dreyer 1933) might cause less osmotic water to be lost in urate excretion than might occur with osmotically active nitrogenous wastes.

The advantages of urate excretion might be evident in two ways in species adapted to either water shortage or high demands for nitrogen (N) excretion relative to water availability: (1) by excretion of a consistently high proportion of urate or (2) by transient increases in the proportion of N excreted as urate, in response to either decreased water availability or high N intake. Regarding the first of these possibilities, previous studies of the proportions of nitrogenous excretory compounds have used only domestic chickens and ducks (e.g., Table II, Shoemaker 1972). While urate accounted for the largest proportion of the waste N in all studies, the percentages of urate-N ranged from 60 to 87% in chickens (see reviews by Sykes 1971, Shoemaker 1972). The only study on ducks (Stewart et al. 1968) reported a low proportion of urate-N (54–57%), and it is tempting to speculate that this is a reflection of an abundant water supply with little selective pressure to conserve water. Studies of wild species with different drinking and feeding habits, and from different habitats, are needed to determine whether patterns of nitrogen excretion show long-range evolutionary adaptations.

McNabb and McNabb (1975a) found no evidence of adaptive changes in the proportion of urate-N excreted by chickens when water availability was reduced to the minimum required for weight maintenance. While water was limited, chickens ate less high protein food rather than increase urate-N excretion. Moreover, studies such as that of Teekell et al. (1968) show no increase in the proportion of excreted urate over the range of 0–14% dietary protein. In contrast, Sykes (1971) presented data which suggest that fed chickens excrete a higher proportion of urate than fasted chickens. However, he gave only mean values from unpublished work, without statistical analysis, and as he did not indicate if water was available, these data cannot be evaluated adequately.

Our objective was to investigate nitrogen excretion in a carnivorous species, the Turkey Vulture (*Cathartes aura*). Vultures feed on carrion which may be far from water. Thus, when feeding under natural conditions, they consume much nitrogen but are limited to that water available in the food. We compared the proportions of urinary N

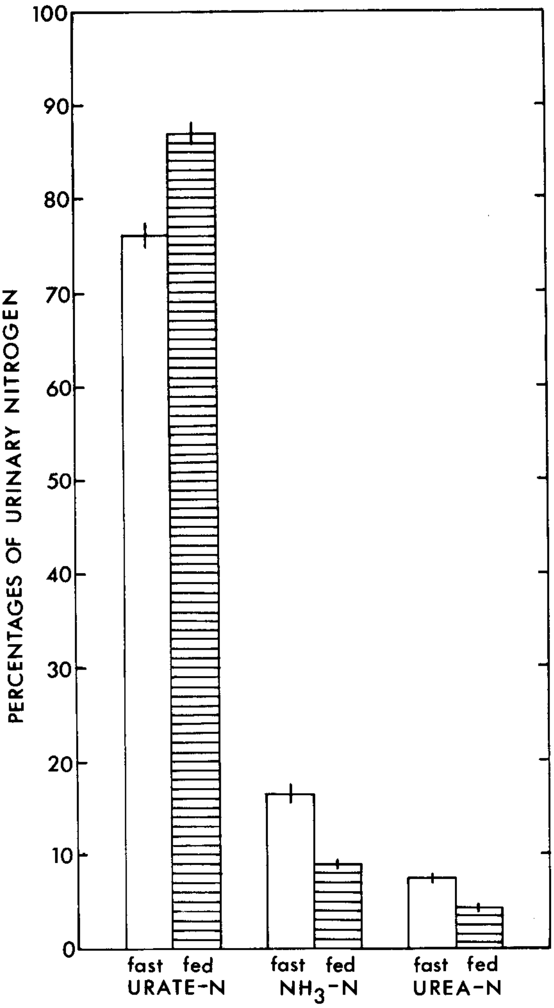

FIGURE 1. The percentages of nitrogen in urate, ammonia, and urea in the urine of Turkey Vultures. Bars are means; vertical lines ± 1 SE. N = 6.

compounds excreted by fasted and fed vultures to determine if feeding resulted in an increase in the proportion of urate-N excreted.

METHODS

Six Turkey Vultures raised in captivity by D. Bittner (Cincinnati, Ohio) were maintained in large outdoor cages (3.1 × 6.1 × 2.4 m) in a wooded area of the Virginia Polytechnic Institute and State University campus. The six birds ranged from one to six years of age, mean body weight was 2.2 kg (range 2.0–2.5 kg), and sex was unknown. The vultures were fed canned dog food (12% crude protein) on alternate days (mean food consumption 280 g/bird at each feeding), with water freely available. Water consumption was not measured. Preliminary studies indicated that the birds could not maintain stable body weights without drinking water during August when this study was conducted.

Urine was collected from each bird for approximately three hours on each of four sequential days. On the first and third days the birds were not fed. On the second and fourth days urine was collected for 30 min, the

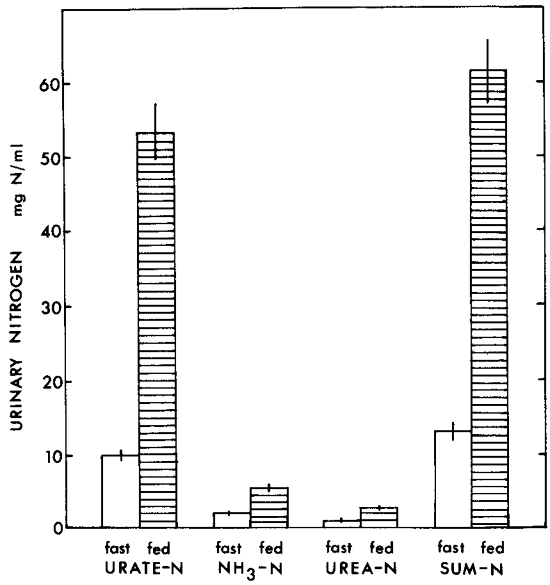

FIGURE 2. Concentrations of nitrogenous compounds in the urine of Turkey Vultures. Bars are means; vertical lines ± 1 SE. N = 6.

birds were fed, and urine collections were continued for at least 1.5 h. The birds did not have access to drinking water at any time during the urine collections. Ambient air temperatures were 24.5–31.5°C; the birds were not exposed to direct sunlight.

For urine collections, the vultures were placed in cages made of plywood and poultry mesh (61 × 76 × 92 cm) with raised mesh floors. Waxed paper was placed under the floor and urine that fell to the paper was collected immediately into capillary tubes. The tubes were sealed, labelled and placed in crushed ice until the end of the collection period, then stored frozen until analyzed. Urine samples with fecal contamination were discarded.

Small urine samples of about 50–100 μl were voided frequently by both fed and fasted birds. We were unable to collect the urine quantitatively, but we did count the number of urine samples voided and we estimated the size of larger drops as multiples of the small drops. This gave an estimate of the relative rates of urine flow for fasted vs. fed birds.

Urine samples were diluted and analyzed for urate, ammonia (NH_3) and urea as described by McNabb and McNabb (1975a). These methods permit the measurement of all three compounds in a single urine sample diluted with lithium carbonate solution to dissolve precipitated urates. Urea (after hydrolysis by urease) and ammonia were determined spectrophotometrically using the indophenol reaction; urate was determined from the fraction of the absorbance at 292 nm abolished by uricase digestion. Osmotic pressures of the urine were determined with a Wescor 5130 vapor pressure osmometer (Wescor Inc., Logan, Utah). Precision levels of the techniques for ten replicates of a single urine sample were such that the SE in each analysis was <0.5% of the mean.

Statistical analyses were performed using Student's *t*-test, with values of $P \leq 0.05$ considered indicative of statistically significant differences.

RESULTS

In the urine of both fasted and fed Turkey Vultures, urate accounted for the highest

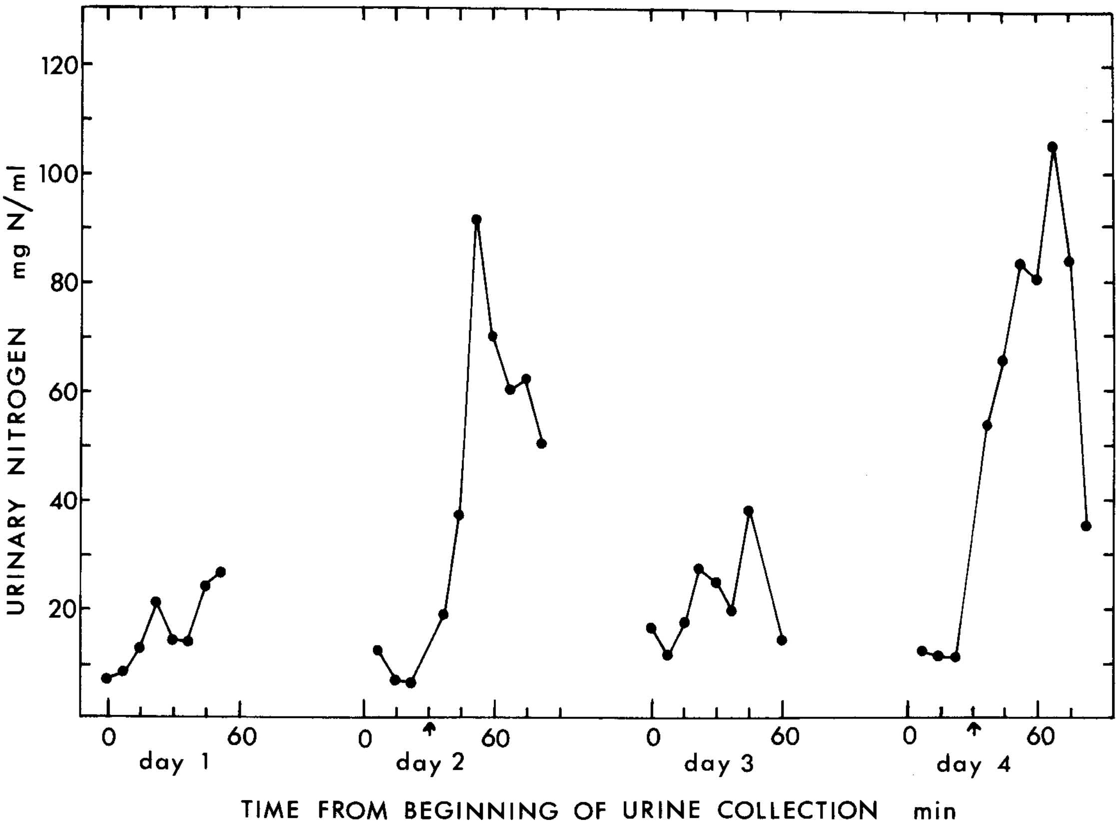

FIGURE 3. The pattern of nitrogen excretion (sum of urate-N, NH_3-N, urea-N) by an individual Turkey Vulture on four sequential days. On days 1 and 3 the bird was not fed; on days 2 and 4 it was given a meat meal (time indicated by arrow) without additional water.

proportion of waste N, followed by NH_3, then urea (Fig. 1). In response to feeding, vultures significantly increased the percentage of urate-N (from 76.1 to 86.8%) and significantly decreased the percentages of NH_3-N and urea-N (Fig. 1).

Urinary concentrations of all three nitrogen compounds increased significantly during the post-feeding period (Fig. 2) but the concentration of urate-N increased 5.5 times while NH_3-N and urea-N concentrations increased only 2.6 times and 2.8 times, respectively. Urinary N concentrations reached maxima 30–45 min after feeding and returned to fasted levels by 1.5 h after feeding (Fig. 3). Each bird exhibited the patterns of N excretion shown in Figure 3 for the two "fasted" and two "fed" days it was studied. The osmotic pressure of the liquid fraction of the urine from fed vultures (417 ± 25 mOsm) did not differ significantly from that for fasted vultures (397 ± 15 mOsm).

The mean rate at which vultures voided urine was 0.29 drops/min for fasted birds and 0.15 drops/min for fed birds (approximately 0.9 and 0.45 ml/h, respectively). These rates are statistically different at $P \leq 0.05$, and indicate a decrease in excretory water losses, in addition to the increased efficiency of N excretion indicated by the increased urinary N concentrations after feeding. Approximations indicate that, during the 1.5 h following feeding, less than 1% of the ingested N actually is excreted.

DISCUSSION

Although meat contains considerable quantities of water, additional drinking water may not be available to carrion feeders immediately after feeding. Because vultures are strong fliers, they presumably can obtain drinking water daily, so they probably do not face extended periods of water deprivation.

Measurements of nitrogen compounds in the urine of fasted Turkey Vultures indicate that the proportion of N excreted as urate (76.1%) is in the middle of the range of values reported for domestic chickens (60–87% of total N excretion; Table II, Shoemaker 1972). Vultures do not consistently exhibit highly "efficient" patterns of N excretion in comparison to chickens. Thus, there is no evidence of long-range, evolutionary adaptation to water shortage in the handling of excretory nitrogen.

However, we did find evidence of an "immediate response" adaptation (terminology of Bligh et al. 1976) exhibited as a rapid, statistically significant increase in the proportion of N excreted as urate in the post-feeding period. This shift in N compounds, and increased concentrations of all N compounds, resulted in a marked increase in excretory efficiency, i.e., 4.8 times more nitrogen was excreted per milliliter of water lost in the urine of fed birds than in the urine of fasted birds. Conversely, when urinary nitrogen concentrations were used to calculate water losses, we found a decrease from 80 ml of water/g N excreted by fasted birds to 16 ml of water/g N excreted by the fed birds. This very low rate of water loss associated with N excretion exhibited by the fed vultures approaches that achieved by the most efficient mammalian kidneys (desert rodents that lose only 9–13 ml water/g N excreted; Schmidt-Nielsen and O'Dell 1961).

After feeding, the marked increase in the proportion of urate-N with concomitant decreases in the proportions of urea-N and ammonia-N appeared to limit the amount of osmotic work necessary for excreting a N load. Thus, osmotic pressures of urine from fed and fasted birds did not differ significantly despite a six-fold difference in urinary nitrogen concentrations. In addition, increased co-precipitation of cations with urinary urates could be another factor in limiting urinary osmotic pressures in recently fed birds. In granivorous birds, as urinary urate precipitation increases, a high proportion of the urinary cations co-precipitate with urate (see McNabb and McNabb 1975b for a summary of the data on chickens; Braun 1978 for data on Starlings, *Sturnus vulgaris*). However, the importance of cation-urate co-precipitation in vultures may not be comparable to the situation in granivorous birds because vultures, like other falconiforms (Cade and Greenwald 1966), appear to possess a nasal salt gland that may eliminate some of their electrolyte load. We observed apparent salt gland secretion during the period after feeding but were not able to collect the secretions without altering the conditions for urine collection.

The urine collection methods used in this study did not allow us to evaluate the relative roles of the kidneys and cloaca in urine concentration. The relatively high frequency of elimination of small amounts of urine seems to indicate that urine remains only briefly in the cloaca, and thus its composition is little modified by that organ. However, since voiding was less frequent after feeding, the high urinary N concentrations at that time could be due partly to an increase in cloacal water reabsorption.

Whether the changes in urinary composition that occur after feeding are due solely to the kidney, or involve some cloacal modification, they do appear to limit the amount of osmotic work necessary for nitrogen excretion. To evaluate this osmotic saving, we calculated the urinary osmotic pressures that would be produced if all urinary N were excreted as urea. This idea was first used by Sykes (1971) who, using data from Hart and Essex (1942), concluded that the excretion of insoluble urates was not an osmotic necessity even with the limited urine-concentrating ability of chicken kidneys. Our present data suggest the opposite, that urate excretion is a necessity for Turkey Vultures. If all the urinary N excreted were present as osmotically-active urea, this would yield about 450 mOsm for fasted vultures, 2,190 mOsm for fed vultures. These calculations indicate that the urinary N of fasted birds, if present solely as urea, would exceed the urinary osmotic pressures we measured; fed birds would need about a five-fold increase in the urine concentrating ability exhibited in this study, to excrete their N in a soluble form. Thus, the excretion of a high proportion of N as insoluble urate appears to be an osmotic necessity for vultures.

The increased efficiency with which Turkey Vultures excrete nitrogen after feeding appears to be an adaptation to carnivory. Although the amount of N excreted at this time is not large (<1% of the two-day food supply provided by the meal was excreted during the 1.5-h collection period), water available in the food is used to excrete N with almost as little water loss as is achieved by the most efficient mammalian kidneys known. While our study does not reveal the mechanisms by which this efficiency is achieved, it does emphasize the existence of a shift toward a higher proportion of urate excretion to achieve this level of excretory efficiency.

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