THE ROLE OF URINARY PRECIPITATES IN THE EXCRETION OF ELECTROLYTES AND URATE IN THE DOMESTIC FOWL

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(Received 15 April 1982 —Accepted 1 December 1982)

SUMMARY

1. In order to quantify losses of Na and K associated with precipitate fractions in semi-solid avian urines, Na, K, uric acid and urates (UA + U) and inulin were measured in plasma, in whole ureteral urine, and in urinary precipitates of hens. Ten animals were used, five fed a control commercial poultry meal (Diet A) and five maintained on a high protein, low-Na feed (Diet B).

2. In ureteral urines from hens on Diet A, dried precipitate accounted for 5-6% of the total whole urine weight, on the average. UA + U constituted about two-thirds of the precipitates' weight and 80% of the total excreted UA + U load of 97-4 mM. The average molar fractions, [Na]/[UA + U] and [K]/[UA + U], in precipitates were in the range 0-1–0-2; and the Na and K lost in these fractions were 12-8 mequiv and 9-6 mequiv, respectively, per 1 whole urine. These losses represent 9% and 23% of total Na and K excretion.

3. Diet B was used to accentuate potential cation loss in precipitates if obligatory binding of K and especially Na were to occur in precipitates. Urinary [UA + U] in whole urine rose to 146 mM of which 95% was found in precipitates. The average molar fraction [Na]/[UA + U], however, fell to 0-06 and that of [K]/[UA + U] to 0-08. Renal loss of Na was 8-5 mequiv and of K was 11-5 mequiv per 1 whole urine.

4. These experiments reveal that significant but minor fractions of excreted Na and K are associated with precipitates of avian urine, although the loss is insignificant compared to that reported in starlings (Braun, 1978). They further indicate that the Na/inulin clearance ratio, based on measurements in whole urine and plasma, adequately reflects fractional excretion which, on Diet A, was 1-8% of the filtered load and, on the Na-poor Diet B, less than 0-1%.

These values place the Na-reabsorbing abilities of these birds easily within the range reported for ureotelic vertebrates and suggest that uricotelism does not impose a major renal salt loss in birds.

INTRODUCTION

Birds and mammals have evolved independently from a now extinct reptilian stock, the cotylosaurs, which flourished about 300 million years ago (Romer & Parsons, 1978).

Key words: Urinary precipitates, birds, uricotelism.
The kidneys of these two extant vertebrate classes have developed some striking novelties when compared with renal function in other vertebrate classes, e.g., elevated and relatively stable glomerular filtration rates, the ability to produce urines more concentrated than plasma, and the reabsorption of a significant fraction of filtered volumes, generally more than 90% (Dantzler & Braun, 1980). Mammals show a greater overall advance in these characteristics than do birds. In contrast to mammals, birds are uricotelic, a metabolic characteristic shared with contemporary reptiles and perhaps retained from a common ancestor.

The excretion of urine containing uric acid and water poses special problems for the renal physiologist. The semi-solid urines consist of a supernatant and a precipitate. The supernatant contains mucoproteins and uric acid and urates (UA + U) in colloidal suspension as well as electrolytes and other dissolved substances. The precipitates contain, principally, UA + U, mucoid substances and electrolytes (McNabb & McNabb, 1975). Any urinary constituent may be unequally divided between the two phases. For example, 40–100 mmol UA + U per l of urine occurs in precipitates and accounts for 60–90% of total UA + U excreted (McNabb, McNabb & Hinton, 1973). Furthermore, the physical chemistry of UA + U and of their association with urinary mucoids in both phases is particularly complex and far from being well understood (McNabb & McNabb, 1980). Analyses of whole urine cannot give a clear idea of the role of either fraction in excretion of a given substance; and the laws of physical chemistry, so successfully applied to the essentially aqueous urines of mammals and amphibians, are apt to produce erroneous conclusions if applied to avian whole urine without regard to the partition of substances between supernatant and precipitate fractions.

In recent years investigation of the separated phases of avian urines has produced results of particular interest concerning the possible role of urinary precipitates in electrolyte excretion. The electrolyte contents of urinary precipitates are commonly reported as molar ratios of electrolytes to UA + U, the major component of precipitates, although it is by no means clear that a direct electrostatic association between urinary cations and anionic urates occurs (McNabb & McNabb, 1975; Dantzler & Braun, 1980). In urinary precipitates of chickens maintained on tap water and fed diets of varying protein and electrolyte content, [Na]/[UA + U] ranged from 0.32–2.74 and [K]/[UA + U] from 0.39–0.68 (McNabb, McNabb & Hinton, 1973). In diuretic starlings the same ratios were 16.5 and 2.1, respectively (Braun, 1978). The precipitates accounted for 43–75% of Na excreted in ureteral urines of chickens and 98.5% in starlings; the corresponding figures for K were 19.2% (chickens) and 84% (starlings). Furthermore, Braun’s calculations revealed that less than two-thirds of filtered Na was reabsorbed from tubular fluid in its passage through starling kidneys.

These results, especially those of Braun (1978), suggest that uricotelism may be responsible for significant differences in renal function in birds (and perhaps reptiles, Minnich, 1976), compared with the handling of Na and K in mammalian and amphibian nephrons (Dantzler & Braun, 1980), the experimental models on which most of our current understanding of renal physiology in vertebrates is based (Pitts, 1974).

These reports form the starting point of our investigation. We have re-examined by clearance studies the renal handling of UA + U, Na, K and water in whole urine and
Urinary precipitates in the fowl

supernatant and precipitate fractions in order to determine the content of these cations and UA + U directly in the precipitates and to calculate the fractional re-absorption of these ions and water.

The experimental animal here was the domestic chicken in a state of normal hydration without diuresis. Our most important findings are molar fractions of [Na]/[UA + U] and [K]/[UA + U] in the range 0.1-0.2, lower than other values reported, and a fractional reabsorption of Na of 0.98, well within the range reported for ureotelic vertebrates. Of the total Na and K loads excreted, significant but minor fractions occur in the precipitates. In these experiments the presence of urinary precipitates does not produce renal loss of monovalent cations beyond that observed in ureotelic vertebrates like mammals and amphibians, where the question of sequestration of electrolytes in precipitates is not relevant.

Some of the work reported here has appeared in abstract form (Long & Skadhauge, 1980).

MATERIALS AND METHODS

Animals

White Plymouth Rock hens (2.8-4.5 kg, average weight 3.5 kg) were housed individually, given food and water ad libitum and a light-to-dark cycle of roughly 12:12 h. Compositions of the two diets used are detailed in Table 1. Five hens were fed a control commercial poultry mix (Diet A), and five were given a high-protein, low-Na feed (Diet B).

Except as noted, all experiments were performed on fed and watered animals. The hens on Diet A consumed approximately 50–60 g/kg body weight⁻¹ day⁻¹ and drank

Table 1. Composition of diets (g kg⁻¹)

<table>
<thead>
<tr>
<th></th>
<th>Diet A</th>
<th>Diet B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein</td>
<td>217</td>
<td>344</td>
</tr>
<tr>
<td>Lipids</td>
<td>26</td>
<td>14</td>
</tr>
<tr>
<td>Nitrogen-free extract substances</td>
<td>521</td>
<td>449</td>
</tr>
<tr>
<td>Cellulose</td>
<td>54</td>
<td>56</td>
</tr>
<tr>
<td>Ash</td>
<td>84</td>
<td>50</td>
</tr>
<tr>
<td>Water</td>
<td>98</td>
<td>87</td>
</tr>
<tr>
<td>Na</td>
<td>2.7</td>
<td>0.7</td>
</tr>
<tr>
<td>Cl</td>
<td>9.0</td>
<td>19.0</td>
</tr>
<tr>
<td>P</td>
<td>2.8</td>
<td>0.42</td>
</tr>
<tr>
<td>Mg</td>
<td>7.8</td>
<td>4.6</td>
</tr>
<tr>
<td>Ca</td>
<td>1.6</td>
<td>2.9</td>
</tr>
</tbody>
</table>

Analyses by Steins Laboratorium (Albertslund, Denmark).
about 100 ml water kg⁻¹ day⁻¹; on Diet B, 40–50 g kg⁻¹ day⁻¹ and 150–200 ml kg⁻¹ day⁻¹.

**Clearance studies**

The hens were weighed and given a first subcutaneous injection of 0.5 ml Ketalar kg body weight⁻¹ (Ketamine HCl, 50 mg ml⁻¹, Parke-Davis); smaller maintenance doses were administered when necessary during the experiments. After being checked for eggs in the oviduct, the hens were placed on their back with their legs fixed to supporting posts and a towel placed lightly over their heads. The animals remained calm throughout the experiments.

Topical anaesthesia (Lidocaine, LEO) was applied to the cloacal region after cleaning, usually necessary in these fed birds; catheterization sites in the legs and wings were injected with Lidocaine. After exposure of ureteral orifices in the cloaca, ureteral funnels were sutured for collection of samples in tared tubules containing chloramphenicol to prevent bacterial degradation of organic urinary constituents. A leg vein for collection of blood samples and a wing vein for priming and maintenance infusions of inulin in Ringer’s solutions were catheterized; in some experiments a wing artery was also catheterized for collection of arterial blood. Body temperature was monitored by a thermistor probe inserted in the breast muscle and averaged 39.9 °C for all experiments; room temperature was 20–24 °C.

Surgical procedures required 30–45 min. After withdrawal of the first blood samples (used as a plasma blank for inulin determinations), a priming dose of inulin (4 ml kg⁻¹ of 10% inulin in 0.3% NaCl) was given and followed by maintenance infusion (5 ml h⁻¹ of 6% inulin in 0.6% NaCl), both delivered by wing vein catheter. Timed urine and blood samples were collected throughout the subsequent periods. The former were collected in test tubes placed in an insulating sheath maintained at body temperature by circulating water. Calculated urine flow rates were normalized for body weight, i.e. ml h⁻¹ kg body weight⁻¹. The clearance studies using inulin began about 90–120 min after the inulin priming dose. Blood pH was measured at 37 °C in anaerobically drawn fresh samples with minimal delay, less than 1–2 min (BMS2/3MK2, Radiometer). Urinary pH was measured at 40 °C with a pH-meter 27 (Radiometer).

The experiments lasted approximately 4 h (10.00 a.m. to 2.00 p.m.) from pick-up to return of animals to their cages, and the hens were observed to be eating and drinking within an hour or two.

Five hens fed Diet A and five hens on Diet B were examined. Some chickens were used twice with at least a month between experiments.

**Sample handling**

Blood samples were immediately centrifuged (3000 r.p.m. for 5 min); the plasma was separated and stored at 2–4 °C until analysis. Urine samples were stored in a water bath at 39 °C until dilution of samples at the end of the clearance studies. At the end of the experiment urine samples were weighed for determination of urine flow and then agitated on a Vortex mixer in an attempt to break up the clumps of solid material before pipetting. 175 µl of whole urine was delivered into tared polyethylene tubes, reweighed and centrifuged at 100 000 g (Beckman Airfuge) for 10 min. As much of the
Urinary precipitates in the fowl

Supernatant fraction was removed as possible, the tubes were reweighed for estimation of the wet precipitates' contribution to whole urine weight ('wet urocrit') and the precipitates were dried to constant weight over CaCl₂ (48–72 h) at room temperature for calculation of the 'dry urocrit'.

Known weights of dry precipitate were redissolved in 0.4 % Li₂CO₃ for determination of electrolyte and UA + U concentrations, i.e. the molar fractions were determined on the samples of redissolved precipitate.

At the end of each experiment, appropriate dilutions of whole urine (at least 1: 50) and of supernatant fractions (at least 1:2) were also made for determinations of UA + U; electrolytes and inulin were also measured in one or both of these samples. Determinations of electrolyte concentrations in whole urine were made on undiluted samples, as were all determinations in plasma with the exception of inulin (1:10 dilutions during deproteinization).

Analyses

Inulin was measured by the anthrone method (Hilger, Klumper & Ullrich, 1958) and uric acid by uricase digestion (Praetorius & Poulsen, 1953) with Zeiss Model DM4 double beam spectrophotometric determination of the reaction products.

Freezing point depression (Model 3R, Advanced Instruments) was used to determine osmolality; and flame absorption photometry (Radiometer, FLM 2) was used to determine [Na] and [K]. For determination of [Na] and [K] in redissolved precipitates the standards contained the same concentration of Li₂CO₃ as did the samples. The average differences in duplicates for inulin and UA + U were 5–6 % and for [Na] and [K] were 1–3 %.

The results discussed below exclude two classes of urine samples analysed: the first samples collected immediately after completion of surgery and those collected at urinary flows greater than 5 ml h⁻¹ kg⁻¹ (considered diuretic). Diuresis was often observed following administration of the inulin priming dose; the average urine flow during these diuretic periods was 9.3 ± 1.4 ml h⁻¹ kg⁻¹.

Tabulated values are given as means ± S.E.M. (number of samples). Statistical comparison of means was performed using Student's t-test. Correlation coefficients (r) were calculated and their significance assessed from a standard table (Simpson, Roe & Lewontin, 1960).

RESULTS

Renal function

Table 2 presents data concerning renal function and the composition of plasma and urine in five hens fed the control diet (Diet A). The large size of the animals permitted collection of samples without imposition of diuresis in these hens which had been eating and drinking at will before the experiments.

Under the conditions of these experiments the hens produced a hypertonic urine characterized by net reabsorption of filtered loads of water (98.4 %), of Na (98.6 %), of K (82.7 %) and net secretion of UA + U (60 % of the excreted load) in whole urine. Urinary pH ranged from 4.74 to 7.25.
Table 2. Renal function and urinary and plasma composition in five hens fed Diet A.

<table>
<thead>
<tr>
<th></th>
<th>Whole urine</th>
<th>Plasma¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>6.10 ± 0.14 (28)</td>
<td>7.42 ± 0.03² (5)</td>
</tr>
<tr>
<td>(UA + U), mmol</td>
<td>97.4 ± 10.7 (28)</td>
<td>0.57 ± 0.07 (5)</td>
</tr>
<tr>
<td>(Na), mequiv/l</td>
<td>138.5 ± 8.3 (27)</td>
<td>155.5 ± 2.4 (5)</td>
</tr>
<tr>
<td>(K), mequiv/l</td>
<td>42.3 ± 3.2 (27)</td>
<td>3.82 ± 0.08 (5)</td>
</tr>
<tr>
<td>Ν, mmol/l</td>
<td>459 ± 27 (31)</td>
<td>323 ± 4 (5)</td>
</tr>
<tr>
<td>V, ml h⁻¹ kg⁻¹</td>
<td>2.16 ± 0.19 (28)</td>
<td></td>
</tr>
<tr>
<td>(U/P) inulin</td>
<td>64.0 ± 6.9 (17)</td>
<td></td>
</tr>
</tbody>
</table>

Means ± s.e.m. (N)

¹Because of the relative constancy of plasma values during experiments, the average value of each experimental animal has been used to calculate the means in this column. N for data under the column 'whole urine' refers to all clearance periods in the five animals.

²Measured in venous blood at 37°C.

Characterization and fractionation of whole urine

The semi-solid character of hen's urine is illustrated in Figs 1 and 2, low and high power (400×) light microscopic images, respectively. The urinary solids consist of spherules and of mucinous strands to which some of the spherules are attached. The spherules range in size from a few to 10 μm and, at this power, show no crystalline forms. Grossly, the supernatant is clear while the precipitate is variegated in colour, from grey-white to yellow. Whole urine, before centrifugation, was viscous; and some strands and clumps of mucin were seen in the fluid. The dried precipitates represented 5.6 ± 1.0% (28) of the whole urine by weight ('dry urocrits'). This fraction of whole urine weight showed a significant, negative correlation with urine flow rates (r = −0.61, N = 28, P < 0.001); i.e. in the more copious urines the precipitate fractions contributed less to total urine weight. The 'wet urocrits' averaged 10.4 ± 1.5% (28), so that water bound to precipitate constituents and that trapped as supernatant accounted for 46% of the weight of the precipitates.

Uric acid and urates

UA + U in whole urine is divided between supernatant and precipitate fractions. The average [UA + U] in supernatants was 17.2 ± 2.4 mmol (28), which represents less than 20% of the total [UA + U] measured in whole urine. The precipitates contained 3.91 ± 0.16 mmol UA + U per g of dried precipitate (28). Since pure uric acid is 5.95 mmol/g⁻¹, about two-thirds of the dried precipitates' weight is composed of UA + U, with the rest due presumably to mucoids, electrolytes and other organic material.

Both urinary flow rates and pH influence the partitioning of UA + U between precipitate and supernatant fractions. [UA + U] in whole urine was negatively correlated with urine flow rate (r = −0.63, N = 28, P < 0.001). This correlation suggests that a fixed amount of UA + U might be excreted at concentrations determined by flow along the nephron. However, urinary pH also appears to play a role as indicated by the positive correlation (r = 0.38, N = 28, P < 0.05) of UA + U excretion rates in μmol h⁻¹ kg⁻¹ and pHU. (pHU and urinary flow rates show no significant correlation in these experiments.) Finally [UA + U] in supernatants, but not in whole urine, w
Fig. 1. Whole urine. Freshly voided hen's urine mounted on a slide and photographed at low magnification. Note the strands of mucoid material.
Fig. 2. Concretions in hen's urine. Photomicrograph of freshly voided hen's urine; 1 scale division = 2.5 μm. The spherical concretions were observed attached to mucoid strands at this magnification.

S. LONG AND E. SKADHAUGE

(Facing p. 47)
Urinary precipitates in the fowl

It is positively correlated with pH\textsubscript{u} \((r = 0.85, N = 27, P < 0.001)\), i.e. the solubility of UA + U decreases in acid urines. In summary, the excretion of UA + U in precipitates was favoured by antidiuresis and acid pH\textsubscript{u}.

**Na and K**

These two ions were the major cations of ureteral urine and with the ammonium ion \([45.6 \pm 5.8 \text{ mequiv} \text{l}^{-1} (28)]\) and accompanying anions can account for most of the osmotically active urinary solutes. In fifteen samples from five hens, [Na] and [K] were less in supernatant fractions than in whole urine, as shown in Table 3. Average ratios of supernatant/whole urine concentrations were 0.85 ± 0.03 for Na and 0.67 ± 0.04 for K. These ratios indicate significant inclusion of Na and K in the precipitate fractions.

The Na and K contents of dried precipitates redissolved in 0.4% Li\textsubscript{2}CO\textsubscript{3} were measured in the same samples used for determination of [UA + U]. The average molar ratio, [Na]/[UA + U], in precipitates was 0.16 ± 0.02 (26); the corresponding ratio for K was 0.12 ± 0.02 (26). The exact values of the low molar ratios for Na and K relative to UA + U reported here are open to question because of the trapping of supernatant in precipitate fractions and the difficulties of measuring the dilute electrolyte solutions of redissolved precipitates. Because of the poor solubility of the dried precipitates, even in Li\textsubscript{2}CO\textsubscript{3}, the solutions were of necessity very dilute, and [Na] and [K] in many samples fell between the lowest standard (0.5 mequiv l\textsuperscript{-1}) and the blank. There was, however, excellent agreement between duplicates. The maximal potential error in the ion concentrations caused by zero point fluctuation was 12–28% for Na, 13–18% for K.

The molar ratios showed significant correlation to the cations' concentrations in whole urines \((r = 0.54\text{ for Na and } r = 0.60\text{ for K}; N = 25\text{ and } P < 0.01\text{ for both})\). This correlation suggests that trapped supernatant may have contributed significantly to Na and K content of the precipitate fractions.

**Effects of diet**

Five hens were fed Diet B (Table 1), a protein-rich, Na-poor poultry feed. Relative to plasma values of hens fed commercial Diet A, plasma composition was largely unchanged except for a decrease in plasma osmolality \((313 ± 1\text{ mosm} (5); P < 0.05)\) and a non-significant increase to 0.93 mm in [UA + U]. The renal contributions to the observed homeostasis of plasma values was reflected in urinary composition. As expected from the diet composition, average urinary pH \((5.12 ± 0.06 (20); P < 0.001)\) and Na \((6.5 ± 0.7\text{ mequiv} (19); P < 0.001)\) were significantly lowered compared to values

| Table 3. [Na], [K] and [UA + U] in paired supernatant + whole urine samples from five hens fed Diet A. |
|---------------------------------|-----------------|-----------------|
| Whole urine          | Supernatant     |                 |
| [Na], mequiv          | 117.0 ± 8.0 (15)| 104.3 ± 6.7 (15)|
| [K], mequiv           | 42.1 ± 5.0 (15) | 29.7 ± 2.8 (15) |
| [UA + U], mm          | 99.1 ± 18.9 (15)| 23.8 ± 3.3 (15) |

Means ± s.e.m. (N).
observed in hens fed Diet A. Furthermore, the range of urinary pH (4-50–5-54) in these experiments was more restricted than in those hens fed the control diet (4-74–7-25). Despite a significant rise in [UA + U] to 145·9 ± 16·8 mM (29) in whole urine (P < 0·05), [UA + U] in the supernatant fraction, 6·4 ± 0·7 mM (19), was lower. This finding is in keeping with the correlation of pHu and supernatant [UA + U] observed in hens on Diet A.

The dry precipitates accounted for 6·4 ± 0·7 % (19) of the total urine weight. The molar ratios in precipitates were [Na]/[UA + U] = 0·063 ± 0·021 (20) and [K]/[UA + U] = 0·085 ± 0·014 (20).

**DISCUSSION**

The primary purpose of these experiments was to quantify the Na and K content in precipitate fractions of an avian urine. This information will permit us to evaluate the importance of urinary precipitates in the overall excretion of these ions and to assess whether uricotelism in birds places greater limits on renal control of Na and K reabsorption than those found in ureotelic animals such as amphibians and mammals.

The hen was chosen as the experimental animal in the present work primarily because its large size assured collection of adequate volumes of ureteral urine without the imposition of an osmotic diuresis, necessary in smaller birds, upon the already artificial conditions of surgery and anaesthesia. We have attempted to minimize post-collection changes in distribution of urinary constituents between precipitate and supernatant fractions by collecting and storing whole urine at body temperature until separation of the two fractions by centrifugation. This procedure was considered important since it has been observed that precipitate formation is favoured by cooling of urine samples even at room temperature.

The composition of whole urines, presented in Tables 2 and 3, is comparable to other results in *Gallus* when fed similar control diets, as are the parameters of renal functions (Skadhauge, 1973, 1977).

In the control hens, inclusion of Na and K in precipitate fractions appears to be significant. The products of the appropriate molar ratio and the [UA + U] in precipitates, estimated as the difference between concentrations in whole urines and supernatants, are 12·8 mequiv Na and 9·6 mequiv K found in the solid phase per 1 of whole urine. These values are probably overestimates since they include ions trapped with the supernatant in precipitate fractions as well as Na and K associated with the urinary solids. These amounts represent 9·3 % and 22·8 % of the excreted loads of Na and K respectively.

Even though a significant fraction of excreted Na and K is associated with precipitate fractions, fractional reabsorption of these ions is high if the clearance ratios calculated from the semi-solid whole urine samples are correct. This appears to be the case since the ionic concentrations in supernatant fractions were significantly lower than those in whole urines in which, furthermore, agreement between duplicates was excellent. Of particular interest here is the Na/inulin clearance ratio, 0·018 ± 0·003 (17), indicating a net reabsorption of 98·2 % of filtered Na in hens on control diets. The K/inulin clearance ratio is 0·212 ± 0·020 (17). The study thus confirms previous observations in several bird species (Skadhuge, 1981, pp. 62–71).
Hens were placed on Diet B for two reasons. The protein-rich, Na-poor diet was intended to increase UA + U excretion and to minimize Na excretion. If major binding of Na were to occur in precipitates, one would expect a greater amount of Na and K to be excreted in association with those fractions in hens fed Diet B than in those fed Diet A. This was not observed. In urines from the former group, only 8.5 mequiv Na and 11.5 mequiv K were excreted in precipitate fractions, despite an increase of 45% in the excreted load of UA + U. The Na in precipitates from hens fed Diet B is less than that from hens fed Diet A by 30%. The increase in precipitate-associated K in hens on Diet B (18%) is equivalent to the increase in precipitate dry weight (19%); this suggests that some of the increase in K content is due to increased trapped volume of supernatant. In the hens fed Diet B, the average Na/inulin clearance ratio was 0.0008 ± 0.0001 (13), demonstrating the well-developed capacity of the hen's kidney to conserve sodium. The average K/inulin clearance ratio was 0.243 ± 0.038 (13) in these animals whose potassium intake was not restricted.

Although one cannot distinguish in these experiments between Na and K trapped in the supernatant and that bound to precipitate constituents, the significant Na/UA + U molar ratio in precipitates of Diet B urines in the presence of low [Na] in whole urines suggests that this ion is in fact incorporated in urinary solids in some manner not entirely dependent on trapping of supernatant. Several possibilities have been suggested (McNabb & McNabb, 1975; Dantzler, 1978), e.g. electrostatic binding of cations to urates and/or anionic groups of proteins and mucopolysaccharides, as well as inclusion within urinary solids dependent on charge densities of precipitate components and urinary cations.

X-ray crystallographic studies (Lonsdale & Sutor, 1971) indicate that only uric acid dihydrate is found in the urinary precipitates of budgerigars, and their finding has generally been accepted for birds as a whole.

McNabb, McNabb & Hinton (1973) have proposed that Na and K are bound to the negative charges of colloidal uric acid and may favour its precipitation with inclusion of the cations in the layers of soluble material observed within the precipitated solids. Finally, one might consider cations to be associated with ionizable radicals of proteins and sulphur-containing mucopolysaccharides added to the tubular fluid in the collecting ducts and ureters (Vogel, Stoeckert, Kroger & Dobberstein, 1965; McNabb, McNabb & Steeves, 1973). This effect, like that proposed by McNabb, McNabb & Hinton (1973), might be expected to show the influence of urinary pH. Neither of these explanations has been substantiated.

A related, unresolved problem is the disparity between our results in hens and those in starlings (Braun, 1978) which may be ascribed to differences in species, in experimental design, or in methodology. Direct measurement of Na and K in precipitate fractions seems to be particularly important here. This was not done in the experiments on starlings but was performed in related studies on quail (Anderson & Braun, 1981). From those data one can calculate molar ratios of Na/UA + U = 0.016 and K/UA + U = 0.125 in precipitate fractions in unanaesthetized and uninfused animals. Precipitate-associated Na and K accounted for 18% and 33% of the total amounts excreted, respectively.

In summary, a significant proportion of excreted Na and K is found in urinary precipitates of hens fed either a commercial diet or a diet rich in protein and poor in
Na. Whether these ions are bound electrostatically to mucoid constituents, include within the layered solids or only the result of supernatant trapped in the solid fraction of the urines cannot be determined by these experiments. It is clear, however, that the kidneys of these birds are capable of reabsorbing the vast majority of filtered Na (more than 99-99% on Na-poor diets), so that their uricotelism does not lead to an obligatory salt-wasting state which would have to be rectified by cloacal resorption. In this they appear as adept as the uricotelic classes of amphibians and mammals.

S.L. received a Fulbright travel grant. The work was supported by NATO research grant no. 1795, and NOVO's fund. Expert technical assistance was rendered by Mrs Pia Hagman and Mrs Mona Nielsen.

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