Effects of water load on renal glomerular and tubular function in desert quail

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BRAUN, ELDON J., AND WILLIAM H. DANTZLER. Effects of water load on renal glomerular and tubular function in desert quail. Am. J. Physiol. 229(1): 222-228. 1975.—Effects of an acute intravenous water load on glomerular and tubular function were studied in the anesthetized desert quail Lophortyx gambelli. Total-kidney glomerular filtration rate (GFR) and single-nephron glomerular filtration rates (SNGFR) of reptilian-type and mammalian-type nephrons increased by more than 50% compared with the GFR and SNGFRs measured during a control mannitol diuresis. Despite the increase in GFR, urine flow rate was only 56% of that in control mannitol diuresis, free-water clearance (C_{\text{H}_{2}O}) remained at 1-2% of GFR, and the animals excreted only about 79% of the water load. More than 99% of the filtered sodium and 93% of the filtered water were reabsorbed during the water load. Possible reasons for the increased GFR and the failure to produce a dilute urine or excrete the water load are discussed.

comparative renal physiology; avian renal physiology; single-nephron filtration rates, Lophortyx gambelli, antidiuretic hormone, arginine vasotocin

THE AVIAN KIDNEY with its heterogeneous population of nephrons provides a unique model for studying the regulation of individual nephron function. The bird kidney contains nephrons that resemble those found in mammalian kidneys and nephrons that resemble those found in reptilian kidneys. The reptilian-type (RT) nephrons are located superficially in the kidney, empty at right angles into collecting ducts, and do not function together to contribute directly to the concentrating mechanism of the kidney. The mammalian-type (MT) nephrons are situated deep compared to the RT nephrons. They have long loops of Henle bound together with vasa recta and collecting ducts into medullary cones. This arrangement, as in mammalian kidneys, appears to permit the avian kidney to produce a concentrated urine (5, 16). The details of these anatomical relationships have been described previously (2).

In previous work with desert quail Lophortyx gambelli, we measured the single-nephron glomerular filtration rates (SNGFR) of both MT and RT nephrons using a modified sodium ferrocyanide technique (2, 3). During a control intravenous infusion of 2.5% mannitol solution, the filtration rates of individual MT nephrons were more than twice those of individual RT nephrons. An infusion of hyperosmotic sodium chloride solution produced a fall in total-kidney glomerular filtration rate (GFR), resulting almost entirely from a reduction in the number of filtering RT nephrons (2). The factors responsible for regulating this reduction in the number of functioning nephrons are not yet completely understood. However, in a second study (3), arginine vasotocin (AVT), the naturally occurring avian antidiuretic hormone, produced a decrease in total-kidney GFR, resulting primarily from a reduction in the number of filtering RT nephrons. This effect occurred with small, probably physiological, doses of the hormone. With large, probably pharmacological, doses of AVT the reduction in total-kidney GFR and in the number of filtering RT nephrons was similar to the reduction that occurred with severe salt loading. However, these large doses also caused changes in the filtration rates of MT nephrons and probably major changes in intrarenal blood flow (3).

In mammalian kidneys the primary effect of antidiuretic hormone is to increase the permeability of the distal nephron to water. Although our previous work (3) with small doses of AVT suggests that one physiological effect of antidiuretic hormone in birds may be to reduce the number of filtering RT nephrons, other workers (1) have obtained evidence of a tubular effect of AVT in domestic fowl. We observed significant tubular effects in desert quail only with larger doses of AVT (3). We felt that small doses of the hormone might not have produced an obvious tubular response because the animals were not in a sufficient water diuresis.

In order to examine further the possible physiological effects of antidiuretic hormone on the avian kidney we water loaded desert quail by infusing them intravenously with a dilute (125 mosmol) glucose-saline solution. The infusion of such a hypotonic solution should have suppressed the release of AVT from the neurohypophysis. During this infusion, we measured total-kidney GFR and the SNGFRs of the MT and RT nephrons as well as the urine flow rate and osmolality. The principal findings were: 1) the total-kidney GFR and the SNGFRs of both populations of nephrons increased significantly compared with those observed previously during the control mannitol diuresis (2); 2) in spite of this increase in GFR, the urine flow rate decreased significantly compared with that during the control diuresis (2); 3) the free water clearance did not change significantly from that observed during the control diuresis (3); and 4) the animals failed to excrete the whole water load infused.
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METHODS

Animals and operative procedures. Desert quail Lophortyx gambelii were used as experimental animals. The quail weighed from 147 to 176 g (mean wt 159 g). They were trapped in their native habitat in the vicinity of Tucson, Arizona (Trapping Permit 73 from Arizona Game and Fish Department) and were maintained in an outside aviary exposed to natural environmental conditions. Eight birds were used in the present study. In captivity, the birds had free access to a cracked-grain mixture and green fodder and were allowed water ad libitum. Operative procedures were essentially the same as those described previously (2). Briefly, the animals were anesthetized with Equi-Thesin (Jensen-Salsbury, Kansas City, Mo.) (3 ml/kg) prior to the operative procedures. A 2% lidocaine solution was used as a local anesthetic during the operations. During the operative procedures and experiments, the birds were restrained by taping their legs and wings to a specially designed bird board. The left brachial vein and artery were cannulated for intravenous infusions and collections of arterial blood samples, respectively. Ureteral urine was collected by exteriorizing the ureters and cannulating them with PE 50 cannulas as previously described (2). Dead space in each ureteral cannula was 18–20 μl.

Renal function studies. To produce a water diuresis, an intravenous infusion of a dilute (125 mosmol) solution of 75 mM glucose and 25 mM NaCl was given at the rate of 0.4 ml/kg per min. This infusion was started without any radioactivity when the brachial vein was first cannulated. The isotope [14C]sodium ferrocyanide) was added to the infusion solution after all the cannulations were completed. Both total-kidney GFR and SNGFR were estimated with [14C]sodium ferrocyanide. The validity of this substance as a marker for estimating glomerular filtration rates in these animals was established previously (2). The single-nephron glomerular filtration rates were determined with the modified Hanssen's (6) technique developed by de Rouffignac, Diess, and Bonvalet (4). A complete description of the technique as modified in our laboratory for use in measuring SNGFRs in avian kidneys has been published previously (2). In the experiments described here, a priming dose of 2 μCi [14C]sodium ferrocyanide (Schwarz/Mann, Orangeburg, N. Y.; sp act 10.9 μCi/mmol) was given followed by a sustained infusion of 20 μCi/ml in the intravenous infusion. At least 40 min were allowed for equilibration of the isotope before the clearance periods were started. Three 10-min clearance periods were taken. By the end of the clearance periods the birds had received 180 min of the intravenous infusion. At the end of the clearance periods, a final arterial blood sample was taken, the body cavity was opened rapidly, and a bolus of 15 μl of a saturated solution of nonradioactive sodium ferrocyanide was injected as a single pulse into the left posterior renal artery through a cannula placed in the left sciatic artery. After a precisely timed interval (about 5 s for these experiments), sufficient to allow the bolus of nonradioactive sodium ferrocyanide to pass about 50% of the distance down the proximal tubule, the blood flow to the kidney was stopped and the kidney was snap-frozen by flooding the entire region with liquid nitrogen. The frozen kidney tissue was then taken for determination of the single-nephron glomerular filtration rates as described previously (2).

Analytical methods. The activity of [14C]sodium ferrocyanide was determined in a liquid scintillation spectrometer (Nuclear-Chicago Corp., Unilux II and Isocap/300). The scintillation solution was the same as that used previously (5). To keep proteins and isolated tubules in solution, the samples or tubule fragments were mixed with 0.5 ml Hyamine hydroxide prior to the addition of 10 ml of scintillation fluid (2). All tubule samples were counted to a minimum of 1,000 counts above background. Total osmolality of plasma and urine samples was determined with a Clifton nanoliter osmometer (Clifton Technical Physics, Hartford, N. Y.). Plasma and urine sodium concentrations were determined with a Baird-Atomic KY-3 flame photometer with internal lithium standard.

RESULTS

Effects of water loading on plasma osmolality and sodium and potassium concentrations. Hydration of the birds with the dilute infusate resulted in a marked decrease in total plasma osmolality (Fig. 1). Although the birds had free access to water at all times prior to the experiments (see METHODS), the plasma osmolality before the start of the intravenous infusion averaged 479 ± 17.1 mosmol (Fig. 1). This value decreased to about 355 mosmol after 75 min of infusion, when about 5 ml of infusate had been given, and remained

![Figure 1](http://ajplegacy.physiology.org/DownloadedFrom)
at this new level during the rest of the infusion period (Fig. 1).

The plasma sodium concentration also decreased after the infusion of 5-10 ml of dilute fluid (Fig. 1). At this time, the sodium concentration had decreased from an initial value of 187 meq/liter to 156 meq/liter. The plasma sodium actually returned to the initial level when 10-15 ml of infusate had been administered and remained at this level during the rest of the infusion period (Fig. 1).

The plasma potassium concentration followed a pattern of change similar to that of the plasma sodium concentration during the period of infusion of the dilute glucose-NaCl solution (Fig. 1). The initial potassium concentration was 8.7 ± 0.95 meq/liter. The concentration decreased to 7.8 ± 1.23 after 5-10 ml of the infusate had been administered. As with the sodium concentration, the plasma potassium concentration returned to the initial level during the time when the total fluid infused increased from 10 to 15 ml (Fig. 1). In contrast to the plasma sodium concentration, however, the plasma potassium concentration again decreased to 7.7 ± 0.72 meq/liter as the total volume of fluid infused increased from 15 to 20 ml (Fig. 1).

The decrease in plasma osmolality was greater than could be accounted for by the combined decreases in plasma sodium and potassium concentrations. Plasma osmolality decreased 124 mosmol from the initial level to that after the infusion of 10 ml of dilute glucose-NaCl solution. The maximum decrease in osmolality that could be attributed to the decreases in plasma sodium and potassium concentrations was about 60 mosmol. Moreover, the plasma sodium and potassium concentrations returned to the initial level while the plasma osmolality remained depressed during the continued infusion.

Effects of water loading on glomerular filtration rates, urine flow, and free-water clearance. Three 10-min clearance periods were taken in the experiments in which the single-nephron as well as the total-kidney glomerular filtration rates were measured. The first period was taken an average of 180 min (11.8 ml infused) after the start of the infusion. An average of 14.9 ml of infusate had been given by the end of the third period.

The total-kidney GFR was 1.390 ± 0.221 ml/kg per min (mean ± SE for 8 animals) during the first clearance period. The GFR during this period was 157% of the GFR observed previously during the infusion of 2.5% mannitol (2) (Fig. 2). The increase over the mannitol control is significant at the 0.001 level of probability. The GFR remained at the increased level during the second and third clearance periods (Fig. 2).

In spite of the high GFR, the urine flow rate was low (Fig. 2). The urine flow rate during the first clearance period was 0.104 ± 0.018 ml/kg per min (mean ± SE for 8 animals). This was only 56% of the urine flow rate (0.186 ± 0.008 ml/kg per min) observed previously during the mannitol diuresis (2) (Fig. 2). The difference in flow rate from the mannitol control is significant at the 0.01 level of probability. The flow rate tended to decrease further during the second and third clearance periods, but the additional decrease was not statistically significant (Fig. 2).

With this low urine flow, the birds only excreted an average of 79% of the fluid infused during the three 10-min clearance periods (Table 1). However, two of the birds (17123 and 2444) excreted over 100% of the fluid infused and two others (2811 and 144) excreted most of the fluid infused. These four birds were in a slight water diuresis, producing a slightly hypotonic urine and a positive free-water clearance (C_H2O). However, the largest positive free-water clearance observed was only 5% of the filtration rate. The remaining four birds excreted a much smaller fraction of the fluid infused (Table 1). One animal (1644) excreted only 38% of the infusate. Some of the infusate not

![Figure 2](http://ajplegacy.physiology.org/)

**TABLE 1. Percent of infusion excreted**

<table>
<thead>
<tr>
<th>Bird No.</th>
<th>Volume Infused*, ml</th>
<th>Volume Excreted, ml</th>
<th>Percent Excreted</th>
</tr>
</thead>
<tbody>
<tr>
<td>18103</td>
<td>0.82</td>
<td>0.404</td>
<td>49</td>
</tr>
<tr>
<td>17123</td>
<td>0.62</td>
<td>1.130</td>
<td>138</td>
</tr>
<tr>
<td>1314</td>
<td>0.39</td>
<td>0.317</td>
<td>53</td>
</tr>
<tr>
<td>2811</td>
<td>1.33</td>
<td>1.174</td>
<td>88</td>
</tr>
<tr>
<td>824</td>
<td>1.26</td>
<td>0.756</td>
<td>60</td>
</tr>
<tr>
<td>144</td>
<td>1.36</td>
<td>1.219</td>
<td>90</td>
</tr>
<tr>
<td>1644</td>
<td>1.18</td>
<td>0.448</td>
<td>38</td>
</tr>
<tr>
<td>2444</td>
<td>1.30</td>
<td>1.509</td>
<td>116</td>
</tr>
</tbody>
</table>

* Volume infused during three 10-min clearance periods. \| Total urine flow over same three 10-min clearance periods.
excreted by these birds appeared to be sequestered within the interstitial fluid compartment, and the birds were edematous at the end of the infusion. These four birds produced a slightly hyperosmotic urine and a slightly negative free-water clearance. The mean free-water clearance for all birds, however, was slightly positive. It averaged about 2% of the glomerular filtration rate during the first clearance period (Fig. 2). This was slightly, but not significantly, greater than the relative free-water clearance (1.6% of GFR) observed previously during the mannitol diuresis (2). During the second and third clearance periods the average free-water clearance decreased to 1% of the glomerular filtration rate (Fig. 2), but this change was not statistically significant.

Effects of water loading on fractional excretion of sodium, potassium, and water. The experimental birds excreted a significantly (P < 0.001) smaller fraction of filtered sodium during water loading than birds previously subjected to an infusion of 2.5% mannitol (2) (Fig. 3). More than 99% of the filtered sodium was reabsorbed by the birds during the water-loading experiments compared with about 94% during the previous mannitol experiments.

The fraction of filtered potassium excretion during water loading was significantly (P < 0.001) greater than that during the infusion of 2.5% mannitol (Fig. 3). About 60% of the filtered potassium was excreted during water loading compared with about 20% during the previous studies with a mannitol infusion (2).

As might be expected from the low urine flow and relative free-water clearance noted above, most of the filtered water was reabsorbed in the present experiments. The percent of filtered water reabsorbed during water loading was significantly (P < 0.001) greater than that observed previously during a 2.5% mannitol infusion (2) (Fig. 3). About 93% of the filtered water was reabsorbed during water loading compared with 78% during the mannitol infusion.

Effects of water loading on single-nephron glomerular filtration rates. The SNGFRs were measured by the sodium ferrocyanide technique in three of the eight birds that were water loaded. In two of these three birds the SNGFRs were very similar (Table 2). The mean values for the SNGFR of the mammalian-type nephrons in birds 824 and 2444 differed by only 0.4 nl/min. This difference is not statistically significant. The mean values for the SNGFR of the reptilian-type nephrons in these two birds also did not differ significantly (Table 2). However, the mean SNGFR for the MT nephrons in bird 1723 was significantly (P < 0.001) higher than that in the other two birds (Table 2). The mean SNGFR for the RT nephrons in bird 1723 was also significantly (P < 0.01) higher than that in the other two birds (Table 2). When the results of the three water-loading experiments are combined, the mean SNGFRs are 33.2 nl/min and 11.4 nl/min for the MT and RT nephrons, respectively (Table 2). These values and the mean values for each individual water-loading experiment are significantly (P < 0.001) greater than the corresponding values obtained previously during a 2.5% mannitol infusion or after the administration of 10 ng of arginine vasotocin per

Table 2. Single-nephron glomerular filtration rates

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bird No.</th>
<th>Mammalian-Type Nephrons</th>
<th>Reptilian-Type Nephrons</th>
<th>Percent Reptilian Type Nephrons Filtrating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water load</td>
<td>1723</td>
<td>53.4 ± 2.46 (50)</td>
<td>15.1 ± 1.77 (48)</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>824</td>
<td>23.8 ± 1.91 (99)</td>
<td>10.1 ± 0.87 (51)</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>2444</td>
<td>23.4 ± 1.35 (56)</td>
<td>9.0 ± 0.91 (47)</td>
<td>100</td>
</tr>
<tr>
<td>Mean*</td>
<td></td>
<td>33.2 ± 1.57 (155)</td>
<td>11.4 ± 0.75 (146)</td>
<td>100</td>
</tr>
<tr>
<td>2.5% Mannitol</td>
<td>14.6 ± 0.79 (27)</td>
<td>6.4 ± 0.20 (41)</td>
<td>71</td>
<td></td>
</tr>
<tr>
<td>10 ng AVT†</td>
<td>11.3 ± 0.89 (102)</td>
<td>4.7 ± 1.05 (31)</td>
<td>52</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SE in units of nl/min; numbers in parentheses are sample sizes. * Mean values of all water load data. † Data presented previously (2).
The potassium concentration measured in the plasma of desert quail is about double that normally found in the plasma of mammals. There was no evidence of hemolysis in the samples, and we have no reason to doubt the accuracy of the determinations. Moreover, similar values have been reported for other avian species (17). In addition, the diet of the desert quail is primarily one of seeds, which are high in potassium content.  

Effects of water load on renal function. In the present study, the total-kidney GFR, the SNGFR, and the number of filtering RT nephrons were significantly higher during an acute infusion of a water load than during the previous infusion of a 2.5% mannitol solution at the same rate (2, 3). A much less significant increase in total-kidney GFR was observed by Skadhauge and Schmidt-Nielsen (15) when unanesthetized chickens were hydrated orally after 36 h of dehydration. The total-kidney GFR in anesthetized chickens during infusion of a dilute solution similar to that used in the present study was somewhat higher than that observed in the unanesthetized, hydrated birds (1).

It should be pointed out that, since the sodium ferrocyanide technique does not permit evaluation of the SNGFR in the same animals before and after an experimental manipulation, the values during a water load in the present study had to be compared with values determined during a mannitol diuresis in other animals. It could be argued that the total-kidney GFR and the SNGFR might have been naturally higher in the present animals than in the previous ones. However, the desert quail studied previously had been captured and maintained under the same conditions as the present animals. In all the animals in the earlier studies the total-kidney GFR and urine flow were virtually identical during the mannitol infusion (2, 3). In previous work (3), we found that arginine vasotocin, the naturally occurring avian antidiuretic hormone, depressed total-kidney GFR and reduced the number of filtering RT nephrons even in small, probably physiological, doses. Some circulating AVT would be expected to be present during a mannitol infusion. Therefore, the increased total-kidney GFR, SNGFR, and number of filtering RT nephrons during the acute water load compared with the mannitol infusion may indicate that the release of AVT was suppressed by the water load. However, the urine flow rate during the water load was only 56% of that during the mannitol diuresis. Since a high urine flow rate could have resulted simply from the osmotic effect of the mannitol, it is even more significant that, in the present study, an average of only 79% of the water load was excreted. Moreover, the free-water clearance averaged only 1–2% of the glomerular filtration rate and did not differ significantly from that during a mannitol diuresis (2, 3). Only 7% of the filtered water was excreted during the water load compared with 22% during the mannitol infusion (2).

A similar water load in anesthetized chickens (1) produced an osmolar urine-to-plasma ratio of about 0.3, a free-water clearance of about 8% of the glomerular filtration rate, and an excretion of 12% of the filtered water. In unanesthetized chickens (15), oral hydration produced a free-water clearance as high as 30% of the glomerular filtra-
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tion rate and led to an average excretion of about 25% of
the filtered water. In these studies with chickens, most of
the increase in urine flow with oral hydration (1,500 %
in unanesthetized animals) or intravenous water loading
appeared to result from a decreased permeability of the
renal tubules to water rather than a significantly increased
glomerular filtration rate. This also appears to be in agree-
ment with the observations that small doses of AVT had a
tubular rather than a glomerular effect in this species (1).

In previous work on desert quail (3), we observed tubular
effects of AVT only with high, probably pharmacological,
doses. We felt that the hormone may not have produced an
obvious tubular response because the animals were not in a
sufficient water diuresis. However, in the present study, a
water load with its attendant depression of plasma osmol-
arity failed to produce a marked water diuresis despite a
high GFR. Even if the primary effect of AVT is to control
GFR in these animals, the increased GFR in the present
study should have produced a marked diuresis unless some
other factor enhanced tubular reabsorption. It is also pos-
sible that the release of AVT from the neurohypophysis
was not suppressed by the water load and that the increase
in GFR resulted solely from a marked expansion of vascu-
lar volume. Even in this case, however, the diuresis should
have been more marked.

In the present study, less than 1% of the filtered sodium
was excreted compared with about 6% during the mannito-
lar diuresis in the previous study (2). Although a greater
excretion of sodium would be expected during a mannitol
diuresis, the reabsorption of more than 99% of the filtered
sodium in the present study is somewhat more than one
might expect in a well-hydrated domestic fowl (14). About
60% of the filtered potassium was excreted in the present
study compared with about 20% during a mannitol diuresis
(unpublished observations). Although the plasma potassium
concentration was very high in the present study, it was also
high in the birds studied previously (6.6 ± 0.72; mean ±
SE for 23 determinations; unpublished observations).

The adrenal function has not been studied in these quail,
but it is possible that the adrenal corticosteroids, especially
aldosterone, may have played a significant role in the
observed excretion of sodium, potassium, and water. In
mammals, high serum potassium concentrations may be
an important direct ionic stimulus to aldosterone secretion
(18). If this is the case in quail, the high serum potassium
may have stimulated aldosterone secretion. If aldosterone
stimulates distal tubule potassium secretion in quail as in
mammals (19), it may have accounted for the high frac-
tional potassium excretion in the present study. It may also
have accounted for the nearly complete reabsorption of
filtered sodium. In mammals, aldosterone can have some
stimulatory effect on proximal tubule sodium reabsorption
(7). If such an effect is marked in quail, it may have ac-
counted for the observed failure to excrete the water load.

Another factor that might play an important role in the
regulation of water excretion in these animals is the au-
terior pituitary hormone prolactin. The renal effects of
this hormone have not been studied in birds. However, it
has osmoregulatory effects in most vertebrates (12) and a
recent report (11) indicates that it can cause an anti-
diuresis in rats with hereditary diabetes insipidus, possibly
by stimulating proximal tubular reabsorption of sodium
and water. In summary, in the present study the water
load may have depressed AVT release, permitting the
marked increase in GFR, but avid isosmotic reabsorption
of sodium and water in the proximal tubule under the
possible control of prolactin or aldosterone may have pre-
vented significant amounts of filtrate from reaching the
distal nephrons where dilution could take place.

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technical assistance.

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