Function of mammalian-type and reptilian-type nephrons in kidney of desert quail

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BRAUN, ELDON J., WILLIAM H. DANTZLER. Function of mammalian-type and reptilian-type nephrons in kidney of desert quail. Am. J. Physiol. 222(3): 617–629. 1972.—Bird kidneys have mammalian-type (MT) as well as reptilian-type (RT) nephrons. Whole-kidney and individual nephron functions were studied in the desert quail during a control diuresis and during 6% NaCl infusion. Glomerular filtration rate (GFR) decreased after ca. 20 mEq NaCl/kg and fell to 20% of control after ca. 40 mEq NaCl/kg. Tubular maximum for para-aminomhippurate secretion decreased with GFR, suggesting that changes in GFR resulted from changes in number of functioning nephrons. Histological data showed 71% of RT proximal convoluted tubule (PCT) lumina open in hydrated birds and 84% lumina closed in salt-loaded birds, suggesting that it was RT nephrons which ceased filtering during salt loading. Single-nephron filtration rates (SNGFR) during control diuresis were 15.8, 10.9, and 6.4 nl/min for large mammalian-type (MT-L), small mammalian-type (MT-S), and RT nephrons, respectively. During salt loading, SNGFR values were 13.4 and 12.4 nl/min for MT-L and MT-S. No RT nephrons were filtering during salt loading. Birds with limited concentrating ability and without salt glands can respond to osmotic stress by reducing number of functioning RT nephrons. Possible regulatory mechanisms for this differential functioning of nephrons and the relationships between SNGFR, PCT length, and glomerular volume are discussed.

Comparative renal physiology, avian renal physiology; desert quail, Lophortyx gambelii; intermittent nephron function; avian single-nephron filtration rates

BIRDS, LIKE MAMMALS, CAN PRODUCE A URINE HYPEROSMOTIC TO THE PLASMA. Although one race of savannah sparrow, which lives in salt marshes, can produce a urine about 5 times the osmolality of the plasma (28), other birds studied cannot produce a urine much more than twice the osmolality of the plasma (4, 23, 28, 38). Gambel’s quail, Lophortyx gambelii, the common desert quail of the southwestern United States, can produce a urine about 2.5 times the osmolality of the plasma (23). The anatomy of the avian kidney suggests that the concentrating ability would not be marked since the medulla is less well developed than in the mammalian kidney. In fact, the avian kidney contains a mixture of nephrons resembling reptilian and mammalian nephrons. Most nephrons resemble reptilian nephrons with simple proximal and distal tubules without loops of Henle and empty at right angles into collecting ducts. However, some nephrons have loops of Henle which, together with vasa recta and parallel collecting ducts, form medullary cones (14, 20, 27, 40, 41). These structures appear to function as countercurrent multipliers, as in mammalian kidneys, to allow the production of a concentrated urine (39).

With only a modest renal concentrating ability, birds are limited in their capacity to reduce plasma osmolality by the renal excretion of salt in excess of water. Although some terrestrial birds do have functional salt glands (3, 33), these desert quail and most other terrestrial birds do not. In what way then do these desert birds, which might be subjected to severe dehydration, respond to an acute osmotic load? Previous work on domestic chickens (7) has indicated that a severe salt load causes a fall in GFR. Moreover, studies of the tubular maxima (Tm) for the secretion of para-aminomhippurate (PAH) and the reabsorption of glucose have suggested that the decrease in GFR results from a decrease in the number of functioning nephrons. This apparent decrease in the number of functioning nephrons raises some intriguing questions concerning birds in general and desert birds in particular (9). First, In those birds which might be subject to severe dehydration, does a filtration rate decrease more readily than in domestic birds? Second, When a decrease in the number of functioning nephrons occurs, does this involve nephrons of both reptilian and mammalian types? We suggested (9) that, if only nephrons of the reptilian type ceased functioning, nephrons of the mammalian type could continue functioning together, allowing maintenance of concentrating ability. Moreover, normal flow through nephrons of the mammalian type would reduce the possibility of urate deposits within the loops of Henle in the medullary cones.

To examine these questions more closely, we subjected Gambel’s quail to a sodium chloride load similar to that used in domestic fowl (7). To evaluate individual nephron function we examined the relationship of TmPAH to GFR, made histological studies, and measured single-nephron glomerular filtration rates (SNGFR) by the modification of Hanssen’s technique developed by De Rouffignac, Diess, and Bonvalet (13). The results indicate that: 1) the overall GFR of Gambel’s quail may be slightly more responsive to an osmotic load than that of the domestic fowl, 2) the filtration rates of individual mammalian-type (MT) nephrons are more than twice those of reptilian-type nephrons during a control diuresis, and, 3) when a decrease in overall GFR occurs, it results from a decrease in the number of filtering RT nephrons.
Animal and operative procedures. Gambels' quail, Lophortyx gambelii, were used as experimental animals. The birds weighed from 140 to 160 g (mean wt: 156 g). The quail were maintained in an outside aviary exposed to natural environmental conditions at Tucson, Arizona. The birds had free access to a cracked-grain mixture and green fodder and were allowed water ad libitum. Animals were placed supine with outstretched wings on a specially designed bird board. The wings were taped to lateral extensions from the board and the feet to vertical extensions of the board. During experiments, the board was tilted to elevate the head board. The wings were taped to lateral extensions from the supine with outstretched wings on a specially designed bird from the brachial artery.

rated by blunt dissection and a PE-10 polyethylene cannula with PE-10 polyethylene tubing. Infusions were given rates were studied, the muscles of the left flank were separated from the brachial artery. Equithesin (Jensen Salsbery, Kansas City, Mo.) was administered as a general anesthesia in a dose of 3.0 ml/kg prior to the operative procedure and 2% lidocaine was used as a local anesthetic during the operations. The left brachial vein and artery were cannulated with PE-10 polyethylene tubing. Infusions were given through the brachial vein and blood samples were collected from the brachial artery.

In experiments in which individual nephron filtration rates were studied, the muscles of the left flank were separated by blunt dissection and a PE 10 polyethylene cannula was placed in the sciatic artery. In birds, the renal arteries which supply the large posterior division of the kidney come off the sciatic artery. The polyethylene cannula inserted into the sciatic artery was advanced in a retrograde fashion to the level of the renal arteries. Its exact position was checked by dissection following the experiments.

The ureters were cannulated by the method of Munnsick, Sawyer, and van Dyke (25). A small incision was made dorsal to the cloacal vent, the ureters were freed by blunt dissection, and a PE 50 polyethylene cannula was tied into each. Dead space in each cannula was 18-20 µl.

Clearance studies. Glomerular filtration rates were estimated as inulin clearances using inulin-carboxyl-14C. A priming injection of 1 µc was given and the blood level was maintained by a constant infusion of 0.06 µc/kg per min. Before the first clearance period 40 min were allowed for equilibration. A control diuresis (mean value ± se of 101 control periods: 0.186 ± 0.008 ml/kg per min from each kidney. Table 1) was produced by a constant intravenous infusion of 2.5% mannitol solution at 0.4 ml/kg per min. When the desired limits of the infusions were reached, the abdominal cavity of each bird was rapidly opened and the kidneys flooded in situ with 10% ice-cold buffered Formalin. The synsacrum of each bird, with the kidneys still in place, was removed and placed in a bath of ice-cold 10% Formalin in which the kidneys were carefully freed from their bony concavity. After fixation in Formalin, the tissue was embedded in paraffin and sections 6-µ thick were cut from it. The sections were stained with hematoxylin and eosin.

Injection and corrosion studies. Corrosion casts of quail kidneys were made by injecting the renal arteries, efferent renal veins, and ureters with Bason's no. 17 anatomical corrosion compound (Polysciences, Inc., Rydal, Pa.). The casts were allowed to harden overnight in distilled water and were then placed in 10% potassium hydroxide to allow corrosion to take place. These studies were used to help reconstruct the anatomy of the quail kidney.

Measurement of individual-nephron glomerular filtration rates. Single-nephron glomerular filtration rates were determined with the modification of Hansen's (17) technique developed by de Rouffignac, Diess, and Bonvalet (13). This technique permits the measurement of filtration rates in nephrons inaccessible to micropuncture techniques and can be carried out in birds without a long exposure of the kidney.

In this technique, carbon 14-labeled sodium ferrocyanide is used as a marker to estimate glomerular filtration rate. The anesthetized birds were prepared as described above. The 14C-labeled sodium ferrocyanide (Schwarz/Mann, Orangeburg, N.Y.; SA: 1 l-32 mc/mmole, depending on the lot used), in a concentration of 20 µc/ml, was infused through a wing vein with the 2.5% mannitol solution or the 6% NaCl solution. A priming dose of 2 µc Na ferrocyanide-14C was given before the start of the sustained infusion, and 40 min were allowed for equilibration before the start of the clearance periods. Preliminary experiments showed that, following equilibration, Na ferrocyanide-14C at plasma concentrations as low as 2.0 × 10⁻³ m gave an estimate of glomerular filtration rate for the whole kidney identical

<table>
<thead>
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<th>TABLE 1. Renal functions during control periods</th>
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<tr>
<td><strong>Experiments with inulin-14C</strong></td>
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<tr>
<td>Urine flow</td>
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<tr>
<td>0.166 ± 0.008 (101)</td>
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<tr>
<td>GFR</td>
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<td>0.892 ± 0.036 (97)</td>
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<tr>
<td><strong>Experiments with Na ferrocyanide-14C</strong></td>
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<tr>
<td>Urine flow</td>
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<tr>
<td>0.121 ± 0.004 (40)</td>
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<tr>
<td>GFR</td>
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<td>0.838 ± 0.093 (40)</td>
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Values are means ± se of milliliters per kilogram per minute. Numbers in parentheses are numbers of clearance periods.

mg/kg per min through the brachial vein with the mannitol and NaCl infusions. The exact plasma PAH concentration at which $T_{\text{mPAH}}$ was reached was not determined in these experiments. However, Dantzler (7) reported that the $T_{\text{mPAH}}$ in domestic chickens was reached at plasma PAH concentrations of 10-20 mg/100 ml.

To study the effect of an osmotic load on renal function, 6.23 mEq/kg of NaCl (as a 6% solution) were given into the brachial vein as a priming injection and the control infusion was replaced with 6% NaCl. The infusion rate of 0.4 ml/kg per min was continued, and an appropriate interval was allowed for the NaCl solution to replace mannitol in the dead space of the infusion system before the first collection period during the salt load was begun. At this rate of infusion, the animals received 4 mEq/kg body wt of NaCl during each ensuing clearance period.

**Histological studies.** Histological sections were made of kidneys taken from birds under the conditions of a control diuresis and of salt loading. The birds were prepared and maintained under anesthesia as described above. The control diuresis was produced by the infusion of 2.5% mannitol and the salt load by the infusion of 6% NaCl at 0.4 ml/kg per min. When the desired limits of the infusions were reached, the abdominal cavity of each bird was rapidly opened and the kidneys flooded in situ with 10% ice-cold buffered Formalin. The synsacrum of each bird, with the kidneys still in place, was removed and placed in a bath of ice-cold 10% Formalin in which the kidneys were carefully freed from their bony concavity. After fixation in Formalin, the tissue was embedded in paraffin and sections 6-µ thick were cut from it. The sections were stained with hematoxylin and eosin.
with that obtained simultaneously using $^3$H-labeled inulin. The control GFR estimated with inulin-$^3$H was 1.046 ± 0.220 (se of four determinations) while the GFR measured simultaneously with Na ferrocyanide-$^{14}C$ was 0.968 ± 0.200 (se of four determinations). At a plasma concentration one-tenth the above value, the clearance of sodium ferrocyanide was only about 75% of the simultaneous inulin clearance, indicating a small saturable reabsorptive process or possibly limited plasma protein binding of ferrocyanide. A similar pattern has been found with rats (2). In the present study, the plasma concentration of sodium ferrocyanide was always well above 2.0 × 10^{-7} M.

After the clearance periods necessary for a control diuresis or a 40 mEq/kg salt load, an arterial blood sample was collected, the abdominal cavity was opened, and the viscera were gently moved to one side to expose the left kidney. A bolus of 15 μl of a saturated solution of nonradioactive sodium ferrocyanide was given as a single pulse through the sciatic artery into the left posterior renal artery. A few seconds were allowed for this nonradioactive sodium ferrocyanide to pass about 50% of the distance down the proximal tubule. Preliminary experiments indicated that this time interval was about 10 sec. At the end of this period, the blood flow to the kidney was stopped and the kidney was snap-frozen by flooding the entire region with liquid nitrogen. No attempt was made to stop the blood flow to the kidney by ligating the renal arteries because they were too fragile. It was assumed that the liquid nitrogen stopped the blood flow to the kidney the moment it contacted the renal arteries. The period from the injection of the nonradioactive sodium ferrocyanide to the stopping of the renal blood flow and the freezing of the kidney was timed to the nearest 0.1 sec. The time from exposing the kidney by opening the abdominal cavity to freezing was about 35–40 sec. Observations of the birds and measurements of arterial blood pressure indicated that this brief period of exposure did not lead to significant deterioration of the animals. The mean arterial pressure measured through the sciatic artery with a P23GB Statham pressure transducer and recorded on a Brush recorder was 115 mm Hg and remained stable when kidneys were exposed for as long as 3 min.

Immediately after freezing with liquid nitrogen, the entire synsacrum with the kidney still frozen in situ was removed and transferred to a dish of ethyl alcohol chilled in Dry Ice. In this bath, the left kidney was dissected free of the synsacrum, fragmented, and transferred to a solution of alcoholic ferric chloride (95 ml ethyl alcohol, 5 ml concentrated HCl, and 30 g anhydrous ferric chloride) at −20 C. The tissue was maintained in this solution at −20 C for 24 hr. During this period a freeze-substitution reaction occurred in which sodium ferrocyanide was converted to insoluble ferric ferrocyanide (Prussian blue). The tissue was then digested for 2.25 hr in 20% HCl at 37 C, washed with distilled water, and refrigerated overnight in a 0.2% ferric chloride−1% acetic acid solution. It was then put in distilled water for at least 4 hr, to soften, before separation of the individual nephrons was attempted. The individual nephrons were isolated using finely drawn glass needles. The nephrons were transferred to a drop of 50% glycerine on a glass slide and their outlines were drawn with the aid of a drawing tube attached to a binocular dissecting microscope. The nonradioactive sodium ferrocyanide could be seen as a band of bright-blue precipitate in the proximal tubule (Fig. 1). The length of the nephrons was determined by tracing the outline on the drawing with a map reader. A filar micrometer on the dissecting microscope was used to measure the glomerular dimensions and the diameter of the proximal tubules.

The nephrons were broken at the front of the bright-blue band of nonradioactive precipitate, and the radioactivity in the nephron from the glomerulus to this point was determined. This radioactivity represented the amount of sodium ferrocyanide filtered from the time the nonradioactive sodium ferrocyanide was given to the time the kidney was frozen. The individual-nephron filtration rate was calculated by dividing the radioactivity filtered during this time by the plasma radioactivity.

Calculation of volume of glomeruli. The shape of the glomeruli of the largest mammalian nephrons appeared to be that of an oblate spheroid with one diameter consistently much longer than the other. Therefore, the formula for the volume of an oblate spheroid was used to calculate the volume of these glomeruli. The diameters of all other nephrons appeared to be equal in any direction and the assumption was made that these glomeruli were spherical for the purposes of calculating their volume.

Determination of number of nephrons. The number of nephrons was determined in nonexperimental kidneys after India ink injections through the renal arteries. Statistical counts of glomeruli were made using the technique of Damadian, Shwayri, and Bricker (6). This was modified so that the final volume of distilled water containing the glomeruli for counting also contained 2.5% Formalin to reduce glomerular breakdown.

Analytical methods. The activities of inulin-carboxyl-$^{14}C$, inulin-$^3$H, and Na ferrocyanide-$^{14}C$ were determined in a liquid scintillation spectrometer (Nuclear-Chicago Corporation, Unilux II). The scintillation solution was the same as that used by Truniger and Schmidt-Nielsen (43). To keep proteins in solution, the samples were mixed with 0.5 ml of Hyamine hydroxide prior to the addition of 15 ml of scintillation fluid. This same system was used for counting the activity in the individual nephrons. The tiny tubular fragments disappeared after mixing with the Hyamine. It was not possible to determine whether these were in solution.
However, counts of a control precipitate of $^{14}$C-labeled ferric ferrocyanide (Prussian blue) showed no change in counting over a period of 24 hr or longer, indicating that there was no change in the physical status of the precipitate in the Hyamine-scintillation solution mixture. Quenching was checked by the internal standard method for all tubule and plasma samples containing Na ferrocyanide-$^{14}$C and was found to be less than 2% in all cases. Consequently, since the calculation of individual-nephron filtration rates involved the ratio of the tubule counts to the plasma counts, quenching could be ignored. All tubule samples were counted to a minimum of 1,000 counts above background. The liquid scintillation system was chosen over the gas-flow counting system used by de Rouffignac, Diess, and Bonvalet (13) when preliminary experiments showed that it gave far greater counting efficiency than the gas-flow system.

Para-aminohippurate concentrations were determined by the method of Friedman, Polley, and Friedman (16) adapted for small samples using Beckman/Spinco equipment (10). Total osmolality of plasma and urine samples was determined with a Fiske osmometer on 0.2-ml samples. Plasma and urine sodium concentrations were determined with a Baird-Atomic KY-3 flame photometer with internal lithium standard.

**RESULTS**

*Anatomy of quail kidney.* The avian kidney is an elongate, flattened organ fitted closely into the bony concavity formed by the synsacrum. The kidney of Gambel's quail is divided into three gross divisions—a large posterior division, a very small middle division, and an anterior division somewhat larger than the middle division.

The types of nephrons, their relative positions in the kidney, and their relationship to other renal structures are shown in Fig. 2. The reptilian-type nephrons (18, 36) are located at the surface of the kidney arranged around a core formed by the central (efferent) vein. The "cylinders" formed by the RT nephrons and central vein form repeating units grouped in radiating patterns from central points over the entire surface of the kidney (Fig. 2).

The majority of the RT nephrons are very simple tubules folded upon themselves 4 times as indicated in Figs. 2 and 3. The structure of the nephrons gradually becomes more complex as the center of each radial group of cylinders is approached on its ventral aspect. The nephrons begin forming more convoluted proximal and distal tubules and intermediate segments resembling loops of Henle.

The RT nephrons drain at right angles into collecting ducts which lie at the periphery of each cylinder (Fig. 2). At least two arteries enter each cylindrical structure and give rise to the afferent arterioles. The capillary tufts within the capsule of the RT nephrons are very simple. The afferent arteriole may enter the capsule, bifurcate, and reunite to form the efferent arteriole (36). Thus, there may be only two capillary loops in the glomerulus of an RT nephron. The efferent arteriole emerges from the capsule and enters a capillary plexus which surrounds the RT nephrons.

Afferent veins which have their origins from within the renal portal system lie near the periphery of each cylinder.
Effects of 6% NaCl infusion on plasma osmolality and sodium concentration. The sodium chloride infusion produced an increase in plasma osmolality of about 12 mOsm/liter for each 4 mEq/kg infused. The control value for the plasma osmolality was 378 ± 2.6 mOsm/liter (mean ± SE of 14 determinations). The plasma osmolality reached a high of 500 mOsm/liter on one occasion after 50 mEq/kg of NaCl had been infused, an increase of 122 mOsm/liter over the control value (Fig. 4). The increase in plasma osmolality could be accounted for by the increase in the plasma sodium concentration (Fig. 4). The control value for plasma sodium concentration was 178 ± 4.2 (mean ± SE of 21 determinations) mEq/liter. The plasma sodium concentration rose as high as 286 mEq/liter, an increase of 108 mEq/liter from the control level, when 50 mEq/kg NaCl had been infused.

Effect of 6% NaCl infusion on urine flow and glomerular and tubular functions. The urine flow remained very near the control level (0.186 ± 0.008 ml/kg per min; mean ± SE of 101 determinations; Table 1) during the early phases of the saline infusion. After 23 mEq NaCl/kg had been infused, the urine flow began to fall and fell to about 20% of the control value when 40 mEq/kg NaCl had been given (Fig. 5).

The glomerular filtration rate followed a pattern similar to that of the urine flow (Fig. 5). The mean control GFR was 0.882 ± 0.036 ml/kg per min (SE of 97 determinations Table 1). The filtration rate remained at, or slightly below, the control value until 23 mEq NaCl/kg had been given at which point the filtration rate began to fall. The fall in GFR was not as rapid initially as the fall in urine flow. However, at the point where they both began to fall (following infusion of 23 mEq NaCl/kg), the mean urine flow was slightly above the control value while the mean GFR was
urine osmolalities equal to or exceeding the corresponding plasma osmolalities (Fig. 4).

This is indicated by diuresis induced by the mannitol and NaCl infusion (Fig. 4). The urine-to-plasma osmolality ratio started to increase and eventually exceeded the control value.

As might be expected, the percent of filtered sodium reabsorbed by the renal tubules decreased during the infusion of the salt load. As can be seen in Fig. 6, the mean sodium clearance increased from about 7.5% of that filtered to about 25%.

Individual nephron function based on TmPAH. It was first suggested by Range et al. (29) that the Tm for glucose could be studied to determine whether changes in GFR resulted from changes in filtration by each glomerulus or from changes in the number of functioning glomeruli. If changes in GFR resulted from changes in the amount filtered by each glomerulus, but all continued to function, the Tm for glucose would not be expected to change. If, however, changes in GFR resulted from changes in the number of functioning glomeruli, the Tm would be expected to vary directly with GFR. Studies on frogs (15, 35) and chickens (7) showed that the Tm for PAH, a substance secreted by the renal tubules, varied with GFR in the same fashion as the Tm for glucose, a substance reabsorbed by the tubules. Although there is now some controversy over the use of TmPAH as a measure of functional tubular mass (12, 42), we have examined the relationship between TmPAH and GFR in the present study.

The tubular maximum for PAH decreased with decreasing GFR, suggesting, according to the classical concept, that glomeruli function intermittently. This relationship is shown for a representative animal in Fig. 7. The mean coefficient of correlation for TmPAH vs. GFR is 0.912 ± 0.019 for 11 experiments.

Individual nephron function based on histological data. If individual glomeruli stopped filtering when GFR decreased, the proximal tubules of these nephrons would be expected to collapse as the remaining filtrate was reabsorbed (34). Therefore, closed proximal tubule lumina would indicate glomeruli that had ceased functioning. An increase in the number of these closed lumina with a decrease in filtration rate would support the concept that changes in overall GFR result from changes in the number of individual functioning glomeruli. To examine this possibility, we made histological sections of kidneys from a bird in a control slightly below the control value (Fig. 3). Like the urine flow, the GFR fell to about 20% of the control value after 40 mEq NaCl/kg had been infused.

With the slightly increased urine flow and slightly decreased GFR during the early phases of the NaCl infusion, the inulin urine-to-plasma (U/P) ratio decreased moderately from the control of 4.7 ± 0.12 (SE of 98 determinations) to a low of 3.2 ± 0.14 (SE of 11 determinations) after the infusion of 25 mEq NaCl/kg (Fig. 6). As both urine flow and GFR fell with continued hyperosmotic NaCl infusion, the inulin U/P ratio started to increase and eventually exceeded the control value.

The total osmolality of the urine increased but remained below that of the plasma in the face of the marked osmotic diuresis induced by the mannitol and NaCl infusion (Fig. 4). The urine-to-plasma osmolality ratio remained quite constant until 35-45 mEq NaCl/kg had been infused. At this point, when urine flow and GFR were quite low, the tubular reabsorption of water increased in spite of the severe osmotic effect of the salt load. This is indicated by urine osmolalities equal to or exceeding the corresponding plasma osmolalities (Fig. 4).

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diuresis and from a bird subjected to an intravenous sodium chloride infusion. The bird in the control diuresis had received 90 min of a 2.5% mannitol infusion at 0.4 ml/kg per min before the kidneys were taken for histology. The animal subjected to a salt load had received 43 mEq NaCl/kg infused as a 6% NaCl solution before its kidneys were taken for histology. At this time, the filtration rate would have been about 20% of the control level (Fig. 5).

Since it appeared most likely that RT nephrons would cease to filter when GFR decreased, sections from superficial areas where only RT nephrons are located were studied. Sections of kidneys from the salt-loaded animal were compared with sections from the same areas of the kidneys from the control animal. The proximal convoluted tubule can be identified easily in cross section in birds, as in mammals, by the presence of a microvillus border.

The sections were examined for the presence of tubules with open and closed lumina. The number of each were counted by two independent observers, one of whom did not know whether the sections came from control or salt-loaded birds, and the results were pooled. The results were expressed as the percentage of proximal tubules with open lumina in any one microscopic field (examined at a magnification of ×450, ca. 32 tubules in each field). On the left side of Fig. 8 is a representative section showing RT proximal convoluted tubules from a kidney of a bird in a control mannitol diuresis. As can be seen in Fig. 8, most of the proximal tubule lumina are open. In the sections examined from the control kidneys, an average of 71 ± 3.1% (SE of 50 determinations) of the proximal tubule lumina were fully open. On the right of Fig. 8 is a representative section showing RT proximal convoluted tubules from a kidney of a salt-loaded bird. As can be seen, most of the tubule lumina are closed. In the sections examined, only an average of 16 ± 2.2% (SE of 58 determinations) of the proximal tubule lumina were fully open. The large number of collapsed tubules in kidneys from salt-loaded birds supports the idea that the observed decrease in GFR results from a decrease in the number of filtering RT nephrons.

Sections through the kidneys cutting across MT proximal convoluted tubules also included RT proximal convoluted tubules. Since it was not possible to differentiate with certainty between RT and MT proximal convoluted tubules in these sections, we compared sections through medullary cones from kidneys from control and salt-loaded birds. As noted above, the medullary cones contain the loops of Henle from the MT nephrons, the collecting ducts, and the vasa recta. Figure 9 shows cross sections of medullary cones from the same kidneys as those shown in Fig. 8. All loops of Henle in these and similar sections from control and salt-loaded animals had open lumina. These observations suggest that MT nephrons continue filtering when GFR decreases.

Individual nephron function based on measurements of SNGFR. Since the TmPAH data and the histological data suggested that some nephrons stopped filtering when the total GFR decreased during the administration of a salt load, we measured the filtration rates of individual nephrons using the modification of Hanssen’s (17) technique developed by de Rouffignac, Diess, and Bonvalet (13). This technique was chosen for several reasons. First, the avian kidney is tightly fitted into the bony synsacrum from which it cannot be freed in the living animal without damage. This alone, would make an approach by micropuncture techniques extremely difficult. Second, the specialized nature of the avian respiratory system makes it difficult to keep the body cavity open for long periods of time. As noted above (see METHODS), this technique requires the opening of the body cavity for only a brief period. Third, a direct micropuncture approach would have permitted study of only the superficial RT nephrons. The present technique permitted identification and study of nephrons from both the reptilian and mammalian populations.

The mean values for SNGFRs for reptilian-type and mammalian-type nephrons during the control diuresis and
During a salt load are shown in Fig. 3. Since all reptilian-type nephrons have a similar structure (Figs. 2 and 3), they were considered as a single group for purposes of presentation. However, for the purpose of summarizing the data, the mammalian-type nephrons were arbitrarily divided into two groups based on the length of the loop of Henle (Fig. 3). The separation was made by listing the lengths of the loops of Henle in rank order. The break was made between lengths of 2.5 and 2.2 mm since no loops had lengths between these values. The mean length of the loop of Henle for the mammalian-type nephrons with long loops (MT-L) was 2.7 mm (Fig. 3). That for the mammalian-type nephrons with short loops (MT-S) was 1.5 mm (Fig. 3). The difference between these lengths is significant at the 0.001 level of probability. The loops of Henle for all mammalian-type nephrons studied ranged in length from 0.7 to 3.7 mm. The mean values for the lengths of the proximal convoluted tubule and the glomerular volumes for these two groups of mammalian-type nephrons were not significantly different.

During the control diuresis, the mean SNGFR for MT-L nephrons was 15.8 nl/min and that for MT-S nephrons was 10.9 nl/min (Fig. 3). The difference between these mean SNGFRs is significant at the 0.01 level of probability. The mean SNGFR for the RT nephrons was 6.4 nl/min (Fig. 3). This is significantly less than that for either the MT-L or MT-S nephrons ($P < 0.001$). Thus, during a control diuresis, a definite gradient existed in the SNGFRs from the MT nephrons with the longest loops to the short RT nephrons. The mean SNGFR for all mammalian-type nephrons combined (14.6 nl/min) (Fig. 3) was also significantly greater than that for the RT nephrons ($P < 0.001$).

Following a salt load of 40 mEq/kg, the mean SNGFR for the MT-L nephrons decreased and that for the MT-S nephrons increased compared with the values during a control diuresis (Fig. 3). Although these changes were not statistically significant, the SNGFR for all mammalian-type nephrons following a salt load (12.7 nl/min) was significantly lower ($P < 0.05$) than that for all mammalian-type nephrons during the control diuresis (Fig. 3).

Following the salt load, no nonradioactive blue ferric ferrocyanide precipitate was found within the lumen or glomerulus of any of the reptilian-type nephrons, and it appeared that the nephrons were not filtering (Fig. 3). Instead, the blue precipitate was found in fine strands lying around the reptilian-type nephrons (Fig. 10). These fine strands, which were not seen when the nephrons were dissected from kidneys during a control diuresis, appeared to represent the peritubular capillaries. Thus, although the nonradioactive pulse of sodium ferrocyanide did not appear to be filtered by the RT nephrons, it did appear to reach the capillary network surrounding them. These data, indicating that the nonradioactive sodium ferrocyanide reached the RT nephrons following a salt load but was not filtered, support the concept that the observed decrease in GFR in salt-loaded birds resulted primarily from a decrease in the number of functioning RT nephrons.

**Relationship between SNGFR and proximal convoluted tubule length.** The relationship between SNGFR and proximal convoluted tubule (PCT) length for all nephrons dissected from the kidneys of animals in a control diuresis is shown in Fig. 11. When both RT and MT nephrons were considered, there was a significant positive correlation between SNGFR and PCT length ($r = 0.7895$ for 64 nephrons). A similar correlation was found for the RT nephrons alone ($r = 0.7562$ for 39 nephrons). However, the correlation between SNGFR and PCT length for the MT nephrons alone was not nearly as marked ($r = 0.3313$ for 25 nephrons).

In Fig. 12 is shown the relationship between SNGFR and PCT length for nephrons isolated from the kidneys of animals that had been subjected to a hyperosmotic saline infusion. Since no SNGFRs could be measured for nephrons of the reptilian type after a salt load, all the data shown are for nephrons of the mammalian type. Again there was a significant positive correlation between SNGFR and PCT length when all nephrons were considered ($r = 0.6247$ for

**Fig. 9.** Photomicrographs comparing sections from medullary cones taken from a hydrated kidney (right) and a salt loaded kidney (left). Magnification is X340 in both cases, but section on left is taken nearer to tip of cone than section on right.

**Fig. 10.** Isolated reptilian-type nephrons showing peritubular capillaries filled with ferric ferrocyanide precipitate (arrows indicate precipitate). X90.
The SNGFR was plotted against the glomerular volume for all nephrons isolated from the kidneys of animals that had been subjected to a hyperosmotic salt load in Fig. 14. Since no RT nephrons that were filtering were dissected from these kidneys, all the nephrons considered were of the mammalian type. When all these MT nephrons from salt-loaded animals were considered (Fig. 14), there was a significant positive correlation between SNGFR and glomerular volume \( (r = 0.6763 \text{ for 64 nephrons}) \). When this same relationship for the individual MT nephrons was considered separately for each salt-loading experiment, however, the correlation was not so marked. The correlation coefficients for the individual experiments were 0.2382 (for 21 nephrons), 0.1134 (for 24 nephrons), and 0.6289 (for 19 nephrons).

**Glomerular counts and relationship of SNGFR to total-kidney filtration rate.** Using the technique of Damadian, Shwayri, and Bricker (6), we found 46,778 \( \pm \) 4,955 (mean \( \pm \) SE of 9 determinations) glomeruli per quail kidney. The very large glomeruli from the large MT nephrons could be differentiated easily from the much smaller glomeruli of the RT nephrons (see data in Fig. 3 for mean glomerular volumes; also note that, because of the way the glomerulus of the RT nephron in Fig. 3 is folded upon the proximal convoluted tubule, it appears to be about twice its actual size). However, the range of glomerular volumes for MT nephrons (Figs. 13 and 14) made it impossible to differentiate the glomeruli of the smallest MT nephrons from those of RT nephrons. Consistently, 10% of the total glomeruli counted were of the very large size from MT nephrons.

Using the mean glomerular count and the mean SNGFR value for different nephron types, we calculated the total-kidney filtration rate. For animals in a control diuresis, we assumed that 10% (4,678) of the nephrons were of the mammalian type and that the mean SNGFR for these nephrons was 14.6 nl/min (Fig. 3). From these figures \( (4,678 \times 14.6) \), we calculated that the filtration rate for all the MT nephrons during a control diuresis was 0.068 ml/min. Assuming that the remainder of the nephrons (42,100...
were of the reptilian type and 71% of these were filtering during a control diuresis (see histological data and Fig. 8) at an average rate of 6.4 ml/min (Fig. 3). From these figures (4,678 × 12.7) we calculated that the MT nephrons would have contributed 0.059 ml/min to the overall GFR of the kidney. Despite the fact that no blue precipitate was seen in any individual RT nephrons examined, we assumed from the histological data (Fig. 8) that 16% of the RT nephrons (6,737) were filtering at an average rate of 6.4 ml/min each (Fig. 3). From these figures (6,736 × 6.4), we calculated that the RT nephrons would contribute 0.043 ml/min to the overall GFR of the kidney. Thus, the overall GFR for the MT and RT nephrons was 0.102 ml/min. The mean GFR for the three salt-loaded kidneys from which these nephrons were taken, determined from the control clearance periods before the kidney was frozen, was 0.209 ± 0.005 ml/min (an of four determinations).

For animals that had received 40 mEq NaCl/kg, we assumed that the 4,678 MT nephrons were filtering at the rate of 12.7 ml/min each (Fig. 3). From these figures (4,678 × 12.7) we calculated that the MT nephrons would have contributed 0.059 ml/min to the overall GFR of the kidney. Despite the fact that no blue precipitate was seen in any individual RT nephrons examined, we assumed from the histological data (Fig. 8) that 16% of the RT nephrons (6,737) were filtering at an average rate of 6.4 ml/min each (Fig. 3). From these figures (6,736 × 6.4), we calculated that the RT nephrons would contribute 0.043 ml/min to the overall GFR of the kidney. Thus, the overall GFR for the MT and RT nephrons was 0.102 ml/min. The mean GFR for the three salt-loaded kidneys from which these nephrons were taken, determined from the last clearance period just before each kidney was frozen, was 0.126 ml/min.

**DISCUSSION**

**Effects of NaCl infusion on GFR for whole kidney.** In the present study, a hyperosmotic sodium chloride infusion produced a marked decrease in glomerular filtration rate in Gambel’s quail. This began early during the infusion and tended to precede slightly the decrease in urine flow rate. The decrease in GFR with a constant infusion of a hyperosmotic saline solution was similar to that observed under similar conditions with domestic chickens (7). In both that study and the present one the decrease in GFR began after the infusion of about 20 mEq NaCl/kg. However, there were some differences between the two studies. In the present study on desert quail, the GFR decreased by about 80% from a control value of about 0.9 ml/kg per min after the infusion of 43 mEq/kg. At this point, the plasma osmolality had increased about 100 mOsm. In the previous study on domestic chickens, the GFR decreased by about 60% from a control value of about 1.2 ml/kg per min after the infusion of 45 mEq/kg. At this point, the plasma osmolality of the chicken had increased about 150 mOsm. These data would suggest that the filtration rate of the desert quail is more sensitive to increases in plasma osmolality than that of the domestic chicken. However, although both the desert quail and the domestic chickens had adequate access to water before the experiments and their weights were stable, the quail may have maintained a naturally smaller extracellular fluid volume compared with the chickens. This is suggested by the observation that, at the start of the experiments, the plasma osmolality of the quail was about 50 mOsm higher than that of the chickens. Maintenance of a naturally smaller extracellular fluid volume and higher plasma osmolality by the quail may have accounted for their lower initial GFR and greater sensitivity to further increases in plasma osmolality. Such differences in hydration might also have accounted for the observation that the same sodium chloride infusion caused a marked increase in urine flow initially in chickens (7) but very little change in desert quail. It should also be noted, however, that the quail in the present study were anesthetized while the chickens in the earlier study were not. This might also explain some differences in sensitivity of filtration rate to an increase in plasma osmolality.

With sodium chloride infusions of less than 20 mEq/kg no effect on GFR was observed. These observations agree with those of Skadhauge and Schmidt-Nielsen (38) on domestic fowl. As suggested by these authors, the increase in plasma osmolality produced by this infusion, which tends to depress GFR, may have been counterbalanced by an increase in extracellular fluid volume, which tends to increase GFR.

**Effects of NaCl infusion on individual nephron function.** The observed decreases in GFR for the whole kidney might have been the result of decreases in the number of functioning glomeruli or the result of decreases in the filtration rates of all the nephrons. The relationship between TmPah and GFR suggests that decreases in GFR in Gambel’s quail result from decreases in the number of functioning glomeruli. This correlation between TmPah and GFR is similar to that observed earlier between TmPah and TmO and GFR in domestic chickens. However, the studies of Deetien and...
Sonnenberg (12) have indicated that TmpPAH may be determined by the intraluminal concentration of PAH and the flow through the tubules. Thus, TmpPAH may not be an adequate indication of functioning tubular mass, in this case, of the number of functioning glomeruli. The findings of Deetjen and Sonnenberg (12) have been challenged recently by the studies of Tanner and Isenberg (42) which do indicate a relationship between TmpPAH and the mass of functioning tissue. Also, the data of Deetjen and Boylan (11) and Rhode and Deetjen (31) suggest that glucose reabsorption is dependent on mass of tubular tissue as well as delivery to tubular sites and possibly electrolyte reabsorption. Thus, the relationship of TmG to GFR does indicate glomerular intermittency in the avian kidney. It could be argued that the collapsed proximal tubule lumina of RT nephrons seen in histological sections from salt-loaded animals were the result of postmortem changes. However, the kidneys from the salt-loaded animals and the animals in a control diuresis were treated in exactly the same manner in preparation for the histology and any postmortem changes should have been present in sections from control as well as salt-loaded kidneys. Moreover, the sections through the medullary cones from both control and salt-loaded kidneys showed no collapsed tubules or other evidence of postmortem changes. Since the medullary cones are deep to the superficial RT nephrons (Fig. 2), they would have been more likely than the superficial nephrons to undergo postmortem changes during the time between the flooding of the kidneys with ice-cold Formalin and their placement in a bath of ice-cold Formalin. Thus, it seems highly unlikely that postmortem changes could have accounted for the histological differences between control and salt-loaded animals.

As noted earlier (see RESULTS), it is not possible to make sections across MT proximal tubules without cutting across RT proximal tubules (Fig. 2). Since the proximal tubules of the two types of nephrons cannot be easily differentiated in histological cross section, only sections through loops of Henle in the medullary cones can be used to indicate if MT nephrons are functioning. Since it is possible that loops of Henle would not collapse even when filtration ceased, open loops of Henle may not be an adequate indication of functioning MT nephrons.

The use of the modification of Hanssen’s (17) technique developed by de Rouffignac, Diess, and Bonvalet (13) has made it possible to determine directly the glomerular filtration rates of individual nephrons of both mammalian and reptilian types. Using this technique, we found that loops of Henle in the medullary cones can be used to indicate if MT nephrons are functioning. Since it is possible that loops of Henle would not collapse even when filtration ceased, open loops of Henle may not be an adequate indication of functioning MT nephrons.

The relationship of SNGFR to total-kidney filtration rate. The factors responsible for regulating this reduction in the number of RT glomeruli in response to rising plasma osmolality are unknown. Arginine vasotocin (AVT), the naturally occurring antidiuretic principle in all birds, reptiles, and amphibians examined (24, 25, 32) appears to regulate the number of functioning nephrons in reptiles (8) and amphibians (19, 44). Earlier studies (7, 37) showed no effect of even massive doses of AVT on avian glomerular filtration rate. However, more recent studies (E. Skadhauge, personal communication) have suggested that AVT may reduce avian GFR. Thus, AVT may act to constrict the afferent arteriole to RT nephrons, reducing the number of functioning glomeruli, and the blood in the main arterial vessels is shunted through the straight bypass vessels into the peritubular capillary network.

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for SNGFrS were somewhat high and that this might be due to ferrocyanide-\textsuperscript{14}C in the tubule walls as suggested by Coelho et al. (5). However, the whole-kidney filtration rate for salt-loaded animals calculated from SNGFrS was only about 80\% of the measured clearance for the same kidneys. If we had assumed that none of the RT nephrons were filtering (a possibility suggested by the examination of the dissected nephrons), then the calculated GFR would have been less than 50\% of the measured clearance. These calculations militate against any significant overestimation of the SNGFr by the ferrocyanide method. Instead, the discrepancies probably are related to the evaluations of the numbers and types of nephrons. The glomerular counts are difficult to perform accurately. Since, as noted above (see RESULTS), it is not possible to differentiate the glomeruli of the smallest MT nephrons from those of the RT nephrons, the proportion of MT nephrons was probably underestimated and the proportion of RT nephrons overestimated. This, alone, would have made a difference in the calculated GFR for the whole kidney. Finally, it was not possible in any given case to know exactly what percentage of the RT nephrons were actually filtering. Even a small change in the percentages used in these calculations, would have made a large difference in the calculated GFR. Thus, considering the possible variables, the whole-kidney GFRs calculated from the SNGFrS are in fairly good agreement with the measured GFRs. Moreover, the agreement between calculated and measured GFR is very similar to that obtained by de Rouffignac, Diess, and Bonvalet (13) for rat kidneys.

Relationship of SNGFr to proximal convoluted tubule length and glomerular volume. Leyssac (21) has suggested that changes in GFR are secondary to alterations in proximal tubular reabsorptive rate. A consistent positive correlation between SNGFr and proximal convoluted tubular length might be taken as some indirect evidence in support of this hypothesis. Baines and de Rouffignac (1) and de Rouffignac, Diess, and Bonvalet (13), employing Hanssen’s (17) technique or a modification of it, did find a significant positive correlation between SNGFr and PCT length and also between SNGFr and glomerular volume in both the laboratory rat and the sand rat, \textit{Pammmomys obesus}. Our data showed similar correlations if the experiments were combined but not if they were considered individually. If we combined the data from the control diuresis experiments, the resulting correlation between SNGFr and PCT length was strongly positive (\(r = 0.7895\)). The same was true of the data from the salt loading experiments (\(r = 0.6247\)). However, as pointed out in the RESULTS, when the data were considered for each individual experiment, the correlation coefficients varied from significantly positive to negative. Also, when the data for combined experiments were considered during a control diuresis, the correlation between SNGFr and PCT length was much stronger for the RT nephrons than for the MT nephrons. In view of the variation among individual experiments and nephron populations in respect to the correlation between SNGFr and PCT length, it is not possible to say that any definite relationship exists.

One might expect to find a high correlation between SNGFr and glomerular volume since the glomerular volume should give some idea of the capillary surface area available for filtration (26). Again a significant positive correlation was found when the data from all control diuresis or all salt-loading experiments were combined. When the experiments were considered individually or, in the case of the control diuresis, when the MT nephrons were considered separately from the RT nephrons, the correlation failed to hold consistently. Because of the variation in these results, it is difficult to consider glomerular volume as a consistent structural indication of filtration rate in these avian kidneys. However, among glomeruli of closely similar size in a single animal, other factors affecting the filtration of individual glomeruli might have prevented a close correlation between glomerular volume and filtration rate.

The significant positive correlations found between SNGFr and PCT length and between SNGFr and glomerular volume when the individual control diuresis or salt-loading experiments were combined may be due to the wide range of individual nephron sizes involved under these circumstances. Baines and de Rouffignac (1) also noted that the SNGFr increased with the size and complexity of the individual nephrons examined.

Of what importance are observed changes in nephron function to desert quail in its natural environment? Like other birds, the desert quail, when subjected to severe dehydration or a salt load, must slow the rise in plasma osmolality. This could be accomplished by the extrarenal excretion of ions, the production of a concentrated urine, the reduction of glomerular filtration rate, or a combination of these. No extrarenal route for the excretion of ions exists in the quail. However, these birds can produce a slightly more concentrated urine than domestic fowl (23, 39). In addition to the production of a concentrated urine, these animals respond to an acute osmotic stress by reducing the number of functioning reptilian-type nephrons. This conserves some additional water at the expense of excreting some waste. However, as in reptiles and amphibians, these small RT nephrons do not function together to contribute to the concentrating ability.

Thus, it appears reasonable that they might cease functioning in times of osmotic stress. At the same time, the MT nephrons continue functioning to produce a concentrated urine. The slight decrease in the filtration of the long-looped MT nephrons may actually contribute to the concentrating process by reducing the rate of flow through the loops of Henle and enhancing the countercurrent multiplication. With a reduced number of functioning RT nephrons, therefore, reduced flow through the collecting ducts in the medullary cones, the concentrating ability may be further enhanced.

In summary, this reduction in number of functioning nephrons, combined with a renal concentrating ability slightly greater than that of the domestic fowl (38) and the closely related \textit{Californiania quail}, \textit{Lophortyx californicus}, and bobwhite, \textit{Colinus virginianus} (23), and possibly a naturally reduced extracellular fluid volume, may be important for the survival of the desert quail in the arid regions of the southwestern United States. These birds have been reported to be able to survive without free water as long as succulent vegetation is available for consumption (22), and they can
utilize saline drinking solutions better than either the California quail or the bobwhite (23).

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