Renal Anatomy in Sparrows From Different Environments

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ABSTRACT The renal anatomy of three species of sparrows, two from mesic areas, the House Sparrow (*Passer domesticus*) and Song Sparrow (*Melospiza melodia*), and one salt marsh species, the Savannah Sparrow (*Passerculus sandwichensis*) was examined. Electron microscopy was used to describe the ultrastructure of the nephron. In addition, stereology was used to quantify the volumes of cortex, medulla, and major vasculature of the kidneys, and the volumes and surface areas occupied by individual nephron components. There appeared to be no differences in the ultrastructural anatomy of the nephrons among the sparrows. Proximal tubules contained both narrow and wide intercellular spaces filled with interdigitations of the basolateral membrane. The thin limbs of Henle contained very wide intercellular spaces which were absent in the thick limbs of Henle. The distal tubule cells contained short, apical microvilli and infoldings of the basolateral membrane. In cross section, the medullary cones of all birds display an outer ring of thick limbs of Henle which surround an inner ring of collecting ducts, which in turn surround a central core of thin limbs of Henle. The Savannah Sparrow has a significantly higher volume of medulla compared to the two more mesic species. Within the cortex, the Savannah Sparrow also has a significantly higher volume of proximal tubules but a significantly lower volume of distal tubules than the other species. Within the medulla, the Savannah Sparrow has a significantly higher volume and surface area of capillaries, and a significantly higher surface area of thick limbs of Henle and collecting ducts than the mesic species. These data suggest that the salt marsh Savannah Sparrow has the renal morphology necessary to produce a more highly concentrated urine than the mesic zone species. J. Morphol. 243:283–291, 2000.   © 2000 Wiley-Liss, Inc.

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The avian kidney is unique in structure among vertebrate kidneys in having two types of nephrons: those with and without a loop of Henle (looped and loopless, respectively) (Braun and Dantzler, 1972). The loopless nephrons stay within the cortex while the looped nephrons extend from the cortex and into discrete medullary areas called medullary cones. Within each cone, the number of loops of Henle decreases as the tip of the cone is approached. This cascade in loop length may aid in establishing an interstitial osmotic gradient along the length of the medullary cones. The intramedullary osmotic gradient facilitates the production of a hyperosmotic urine by the passive reabsorption of water from the collecting ducts as they pass through the interstitium of the medullary cones (Layton, 1986; Nishimura et al., 1989; Layton and Davies, 1993; Layton et al., 1997).

Birds and mammals are the only classes of vertebrates that are consistently able to produce a hyperosmotic urine. In birds, this ability to produce a hyperosmotic urine is limited compared to that of mammals. The urine-to-plasma osmolality ratio (U/P ratio), a measure of concentrating ability, in birds ranges from 0.2 in Anna's Hummingbird to 3.0 in the Budgerigar, with most species having a ratio of about 2.0 when they are deprived of water

(Table 1). In contrast, the U/P osmolality ratio of mammals spans a broad range from about 1.8 in the Mountain Beaver (*Aplodontia rufa*) (Schmidt-Nielsen and Pfeiffer, 1970) to 26.8 in the Desert Hopping Mouse (*Leggadina hermanburgensis*) (MacMillen and Lee, 1967). The reason for the limited urine-concentrating ability in birds compared to mammals is uncertain; however, it may be related to the fact that most of the nephrons within the avian kidney are of the loopless type. Without a loop of Henle, urine cannot be concentrated, and as all nephrons within the avian kidney (regardless of type) empty into a common collecting duct, the fluid from the loopless nephrons may be diluting the fluid from the looped nephrons.

Despite numerous studies undertaken, no good index has been found that correlates anatomical structure and the ability to concentrate urine in either birds or mammals. Most studies have concen-

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TABLE 1. Urine to plasma osmolality ratios among birds

Species	Habitat	U/P ratio
Budgerigar[4]	domestic	0.3–3.0[u]
Domestic fowl[5,6]	domestic	1.6–2.1[u]
Ring-necked pheasant[3]	domestic	0.6–1.5[u]
Kookaburra[1]	wet	2.3–2.7[v]
Singing honeyeater[1]	wet	2.3–2.4[v]
Red wattlebird[1]	wet	2.0–2.4[v]
Bobwhite quail[6]	mesic	1.6
California quail[6]	mesic	1.7
Senegal dove[1]	mesic	1.7[v]
House sparrow[8]	mesic	1.0–1.7[u]
Song sparrow[8]	semi-arid	0.7–2.2[u]
Anna's hummingbird[7]	semi-arid	0.2–0.6[f]
Rufous hummingbird[7]	semi-arid	0.2–1.1[f]
House finch[6]	semi-arid	2.1–2.3
House sparrow[3]	semi-arid	1.0–2.2[u]
White-crowned sparrow[3]	semi-arid	1.3–2.1[u]
White-winged dove[3]	semi-arid	1.2–1.8[u]
Crested pigeon[1]	arid	1.7–1.8[v]
Emu[1]	arid	1.1–1.4[v]
Galah[1]	arid	2.1–2.5[v]
Gambel's quail[6]	arid	2.5
Zebra finch[3]	arid	1.1[u]–2.8[v]
Glaucous-winged gull[3]	marine	1.6–1.9[u]
Savannah sparrow[2]	salt marsh	1.6–2.7[f]

[f] Field samples, [u] ureteral, [v] voided.
[1] Skadhauge, 1974.
[2] Goldstein et al., 1990.
[3] Goldstein and Braun, 1989.
[4] Krag and Skadhauge, 1972.
[5] Skadhauge and Schmidt-Nielsen, 1967.
[6] Reviewed in Dantzler, 1970.
[7] Beuchat et al., 1990.
[8] Data from present study.

trated on the kidneys of mammals and are summarized in detail by Beuchat (1996). Briefly, indices examined in mammals include absolute medullary thickness, relative medullary thickness, and length of the loop of Henle. The summary presented by Beuchat (1996) indicates that for mammals urine concentrating ability is not a simple function of the length of the loop of Henle, nor of any other single variable measured, and that a number of other variables may be involved. For birds, similar morphological indices have been examined in an attempt to find a relationship between structure and function with respect to concentrating ability. These include relative thickness of the renal medulla (Johnson, 1974), relative medullary area (Sperber, 1944), percent of looped nephrons and the number of medullary cones (Goldstein and Braun, 1989), and the lack of the thin ascending limb in the avian nephron (Beuchat, 1990). As in mammals, these variables are not strongly correlated with the ability to produce a concentrated urine.

In birds, available data on urine concentrating ability are limited, hence this makes it difficult to find a correlation between urine concentrating ability and renal morphology (Table 1). It might be expected that an animal inhabiting an arid environment would have a greater ability to concentrate the urine; however, the present database is insufficient to allow such a conclusion to be drawn. Birds inhabiting arid environments may not always produce the most concentrated urine (Table 1).

Our study presents data on the renal morphology of three species of sparrows, two from mesic habitats and one inhabiting a salt marsh area. Our aim is to highlight the morphology of the kidneys of birds from different environments in an attempt to correlate differences in renal anatomy with habitat and published data on renal concentrating ability for these species. The gross and microanatomy of the kidneys are described and the volumes and luminal surface areas of the nephron components are quantified using stereological techniques.

MATERIALS AND METHODS
Animals

Sparrows (males and females) used in this study were taken from two different areas. Two species, the House Sparrow, *Passer domesticus,* and Song Sparrow, *Melospiza melodia,* were collected in the field in Pennsylvania, under state license, using mist nets. These birds were transported in cages back to the laboratory for processing of tissue on the day of collection. A third species, the Savannah Sparrow, *Passerculus sandwichensis,* was collected in Baja California by E.J. Braun. Mean body mass of the birds was: House Sparrows 26.5 ± 1.3 gm (n = 6), Song Sparrows 20.5 ± 1.3 gm (n = 5), and Savannah Sparrows 18.7 ± 1.8 gm (n = 5).

U/P Ratios

Upon capture of the House and Song Sparrows, ureteral urine was collected with small close-ended cannulas (constructed from micropipette tips) containing an opening that was placed over the ureteral orifices. A sample of whole blood was taken from the brachial vein of each bird. Both urine and blood samples were placed on ice until transported back to the laboratory. The urine was tested for osmolality using a vapor pressure osmometer (Wescor, Utah). Whole blood was centrifuged and the plasma extracted and tested for osmolality using the osmometer. The osmotic concentration of urine to plasma was then calculated.

As noted earlier, the Savannah Sparrow kidneys were donated by E.J.B. from another study (Goldstein et al., 1990). Urine to plasma osmolality ratios were calculated in the same manner in that study and the data are presented in Table 1.

Animal Preparation

Birds were killed with an overdose intraperitoneal injection of sodium pentobarbital, the abdominal cavity opened, and the dorsal aorta cannulated. The kidneys were flushed with 0.2 M phosphate buffer (pH 7.4), followed by half-strength Karnovsky's fix-

ative (350 mOsm). After fixation, the kidneys were dissected from the synsacra.

Electron Microscopy

Kidney tissue was prepared as described above. The left kidneys of House Sparrows and Song Sparrows were processed for scanning (SEM) and transmission electron microscopy (TEM). Tissue for SEM was postfixed in 1% Dalton's osmium tetroxide, dehydrated in a graded series of alcohols, and critically point-dried. The tissue was fractured with a sharp knife, placed on aluminum stubs, sputter-coated with gold, and viewed with a scanning electron microscope. Tissue for TEM was cut in 1 mm^3 blocks, postfixed in 1% Dalton's osmium tetroxide, washed in a series of graded alcohols, infiltrated with propylene oxide, and embedded in epon resin. Sections were cut to a thickness of 90 nm, stained with uranyl acetate and lead citrate, and viewed with a transmission electron microscope.

Light Microscopy

The right kidneys were processed for light microscopy. Prior to processing, the lengths and widths of the kidneys were measured to ±0.01 mm using vernier calipers and their volumes estimated by water displacement (Scherle, 1970). The tissue was then processed for routine light microscopy. Following processing, the lengths and widths of the kidneys were remeasured and the amount of shrinkage due to processing determined. Linear tissue shrinkage ranged from 10–30%, which is within the range reported in previous studies (Casotti and Richardson, 1992, 1993a; Casotti et al., 1998). The tissue was embedded in paraffin wax and cut in an unbiased manner at 10 equally spaced intervals along its length (Mayhew, 1991). The resulting sections were stained with hematoxylin and eosin.

Volume densities (V_v) of the kidney components (cortex, medulla, major blood vessels) and nephron components (renal corpuscle, proximal tubule, loops of Henle, distal tubule, collecting ducts) were estimated by point counting using the Cavalieri Principle from light microscopy tissue (Gundersen et al., 1988). These were converted to absolute volumes by taking into account the volume of the kidney estimated by water displacement. The surface areas of renal tubules were estimated using the formula [(V_v/d) $\times$ 4] $\times$ reference volume from light microscopy tissue (Gundersen, 1979). Where V_v is the volume of the component measured by the Cavalieri Principle, d is the mean luminal diameter of the component measured, and reference volume refers to either the cortex or medulla, depending on whether the component measured occurs in the cortex or medulla. Measuring both volumes and surface areas enabled determining whether differences in kidney structure were due to the presence of either bigger tubules or a greater total length of smaller tubules.

Statistics

Volume and surface area data were analyzed using analysis of covariance (MANCOVA) to correct for variations of body mass using the statistical software program Statistica. In order to correct for the allometric effect of size on variations such as body mass and kidney volume among birds, all measurements were log transformed and regressed against the appropriate size covariate. Different independent variables were used depending on the dependent variable being measured. For example, when analyzing differences in kidney volume, bird body mass was used as the independent variable. When comparing the volumes of the cortex, medulla, and major blood vessels, kidney volume was used as the independent variable. When comparing the volumes and surface areas of the renal corpuscle, proximal tubules, distal tubules, cortical collecting duct, and cortical capillaries, the volume of the cortex was used as the independent variable. When comparing the volumes and surface areas of the limbs of Henle, collecting ducts, and medullary capillaries, the volume of the medulla was used as the independent variable. To compare differences between slopes and elevations of regression lines a Student-Newman-Keuls (SNK) test was performed (Zar, 1984).

RESULTS

This study was carried out in an attempt to correlate the structure of the avian kidney with habitat in three small passerine birds of similar body mass, coming either from different habitats or different lineages. The Song Sparrow and the Savannah Sparrow are more closely related, but from different habitats, and the Song Sparrow and House Sparrow are from similar habitats, but not as closely related.

External Morphology

In external morphology, the kidneys from the three species are very similar. Each kidney consists of three divisions, a large posterior, a small middle, and an anterior division somewhat larger than the middle division. This gross anatomy is very similar to that described for the desert quail (Braun and Dantzler, 1972).

Volume of Kidney Components

The volume occupied by the cortex did not differ among the species. However, the volume of the medulla was significantly higher ($P < 0.05$) in the Savannah Sparrow kidney compared to that of the other two species. Also, the Savannah Sparrow kidney had a significantly lower ($P < 0.05$) volume of

TABLE 2. Mean (± SD) absolute volumes of the right kidney and its associated components

	Volume (mm^3)			
Variable	House Sparrow	Song Sparrow	Savannah Sparrow	Statistics
Kidney	126.6 ± 8.0 (0.94)	129.4 ± 18.6 (1.14)	129.8 ± 49.1 (1.22)	ns
Cortex	99.5 ± 6.7 (1.0)	109.5 ± 16.6 (1.03)	108.7 ± 35.1 (1.03)	ns
Medulla	9.3 ± 3.4 (0.93)	6.8 ± 1.5 (0.81)	15.2 ± 13.6 (1.09)	S[1]
Major blood vessels	17.7 ± 7.8 (1.21)	13.1 ± 2.7 (1.11)	5.8 ± 1.7 (0.76)	S[2]

Data in parenthesis are adjusted log$_{10}$ mean (y) values for regression analyses.
ns = not significant, s = significant.
[1] Savannah Sparrow > House, Song Sparrow.
[2] House, Song Sparrow > Savannah Sparrow.

T2 major blood vessels than did the other species (Table 2). Within the cortex, the Savannah Sparrow kidney had a significantly higher ($P < 0.01$) volume of prox-imal tubules, but a significantly lower ($P < 0.01$) volume of distal tubules than the other species (Ta-**T3** ble 3). Also, the Song Sparrow had a significantly higher ($P < 0.01$) volume of capillaries in the cortex than the other species. For ease of visualization of the volume data among species, the data were con-**F1** verted to percentages and graphed in Figure 1.

Surface Area of Kidney Components

When comparing surface areas of cortical compo-nents, the Savannah Sparrow had a significantly higher ($P < 0.01$) surface area of proximal tubules than did the other two species, and the House Spar-row had a significantly lower ($P < 0.01$) surface area of capillaries than did the other species. There were no significant differences in the surface areas of the other cortical nephron components among the spe-cies. Within the medulla, the Savannah Sparrow kidneys had a significantly higher surface area of thick limbs of Henle ($P < 0.001$) and collecting ducts **T4** ($P < 0.001$) than did the other species (Table 4). The

Savannah Sparrow kidneys had a significantly higher ($P < 0.05$) surface area of proximal tubules than did the Song and House Sparrow and the Song and Savannah Sparrows had a significantly lower ($P < 0.05$) surface area of thin limbs of Henle than did the House Sparrow (Table 4).

Qualitative Morphology

In cross section, the tubules of the medulla display an ordered arrangement. An outer ring of thick limbs of Henle surrounds a ring of collecting ducts, that in turn surrounds a central core of thin limbs of Henle (Fig. 2). **F2**

For all birds, the diameter of the renal corpuscles ranged from 20–48 µm. The glomerular capillaries are centrally located within the renal corpuscle and are surrounded by podocytes. The podocytes branch forming primary (trabeculae) and secondary (pedi-cels) processes (Fig. 3a,b). The proximal tubule is **F3** connected directly to the renal corpuscle and no neck segment is present. The cytoplasm of the proximal tubule cells contains numerous mitochondria, con-densing vesicles, and a large apically situated nu-cleus. The intercellular spaces of the proximal tu-

TABLE 3. Mean (± SD) absolute volumes of nephron components of the right kidney

	Volume (mm^3)			
Variable	House Sparrow	Song Sparrow	Savannah Sparrow	Statistics
Cortex				
Renal corpuscle	2.9 ± 0.9 (1.46)	1.5 ± 0.6 (1.13)	1.3 ± 0.5 (1.11)	ns
Proximal tubule	54.3 ± 6.6 (0.75)	54.0 ± 6.3 (0.71)	71.2 ± 20.0 (0.84)	S[1]
Distal tubule	17.5 ± 3.1 (1.25)	18.8 ± 7.5 (1.23)	11.0 ± 2.2 (1.03)	S[2]
Collecting duct	4.4 ± 1.7 (0.64)	4.8 ± 0.9 (0.65)	4.3 ± 3.6 (0.43)	ns
Capillaries	20.7 ± 5.2 (0.33)	30.4 ± 4.3 (0.45)	22.2 ± 11.8 (0.30)	S[3]
Medulla				
Proximal tubule	0.02 ± 0.02 (0.42)	0.6 ± 1.1 (0.78)	0.02 ± 0.03 (0.70)	ns
Thin limb of Henle	0.6 ± 0.3 (1.84)	0.2 ± 0.03 (1.55)	0.5 ± 0.7 (1.38)	ns
Thick limb of Henle	3.9 ± 1.5 (0.56)	2.8 ± 0.8 (0.53)	6.4 ± 4.9 (0.59)	ns
Collecting duct	2.9 ± 1.2 (0.43)	1.7 ± 0.2 (0.34)	4.3 ± 3.6 (0.40)	ns
Capillaries	1.9 ± 0.6 (1.26)	3.0 ± 0.5 (1.43)	2.1 ± 4.5 (1.30)	ns

Data in parenthesis are adjusted log$_{10}$ mean (y) values for regression analyses.
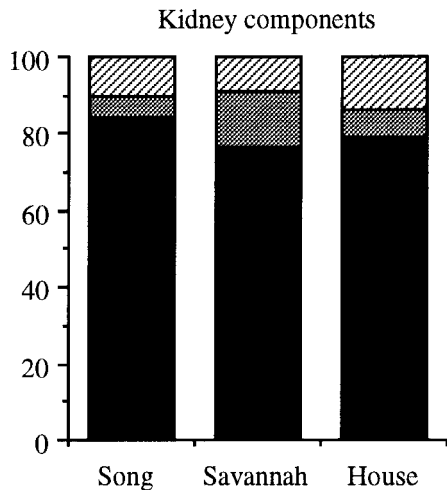ns = not significant, s = significant.
[1] Savannah Sparrow > House, Song Sparrow.
[2] House, Song Sparrow > Savannah Sparrow.
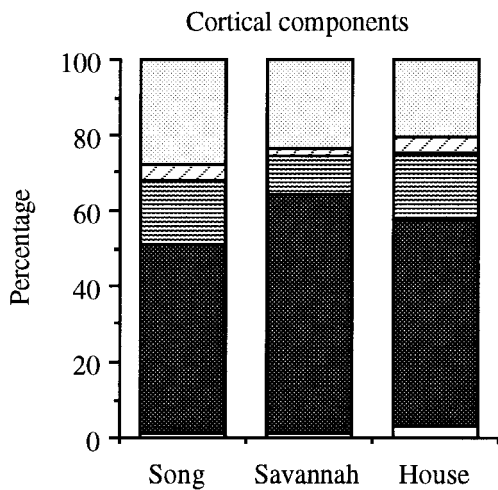[3] Song Sparrow > House, Savannah Sparrow.

Kidney components

Cortical components
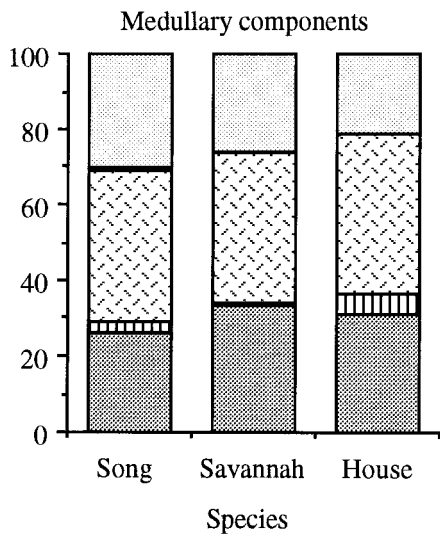

Medullary components

Fig. 1. Percentage volumes of cortex (■), medulla (▨), major blood vessels (▨), renal corpuscle (□), proximal tubule (■), distal tubule (▤), cortical collecting duct (▨), cortical capillaries (▨), medullary collecting duct (▦), thick limb of Henle (◨), thin limb of Henle (▥), medullary proximal tubule (▨), and medullary capillaries (▨) within the kidneys of sparrows.

bules show varying degrees of expansion and are filled with interdigitations of the basolateral membrane (Fig. 4a,b). The apical surface of the proximal tubule cells is enhanced by a prominent microvillus brush border.

The transition from the proximal straight tubule to the thin descending limb of Henle is abrupt (Fig. 4b). The cytoplasm of the thin limb of Henle cells contains few small mitochondria, and the cells are separated by wide intercellular spaces. As with the proximal tubule, the transition from the thin limb of Henle to the thick limb of Henle is abrupt. The cytoplasm of the thick limb of Henle cells contains a higher population of mitochondria than that of the thin limb of Henle. The apical surface of the cells is relatively undifferentiated (Fig. 5).

The cytoplasm of the cells of the distal tubule contains numerous rounded and longitudinal mitochondria throughout. The cells possess infoldings of the basal membrane and narrow intercellular spaces. The apical surface of the cells is covered with a short, thinly dispersed layer of microplicae (Fig. 6). As is the case for mammals, the avian cortical collecting ducts contain two types of cells, the principal and intercalated cells. The apical surface of the principal cells is covered by a thick layer of stubby microvilli and the apical surface of the intercalated cells is covered with microplicae and a single cilium (Fig. 7). The cortical collecting duct continues into the medulla as the medullary collecting duct, and the apical morphology of the cells changes. The apices of the cells protrudes prominently into the lumen and may be covered with very low or small microplicae and a single cilium protruding from each cell (Fig. 8).

DISCUSSION

The data from this study show differences in the internal morphology of the kidneys of the salt marsh Savannah Sparrow compared with those of the mesic-inhabiting Song and House Sparrows. However, the data are not consistent with the assumption that the salt marsh species would produce the most concentrated urine. This is not surprising, given that the U/P osmolality ratio for two of the species show some degree of overlap: House Sparrow 1.0–2.2, Song Sparrow 0.7–2.2, and Savannah Sparrow 1.6–2.7 (see Table 1).

All species showed the same ordered arrangement within the medullary cone, where the thick and thin limbs of Henle were separated by the collecting ducts. This pattern is common among passerines; however, its functional significance is not understood (Johnson and Mugaas, 1970; Johnson, 1979; Goldstein and Braun, 1986; Nishimura et al., 1989). The current theory of the mechanism of urine concentration in birds states that an osmotic gradient is established along the length of the medulla by the transport of solutes from the thick limb to the med-

TABLE 4. Mean (± SD) absolute surface areas of nephron components of the right kidney

Variable	Surface area (cm²)			
	House Sparrow	Song Sparrow	Savannah Sparrow	Statistics
Cortex				
Renal corpuscle	2.0 ± 0.6 (1.32)	1.4 ± 0.6 (1.05)	1.6 ± 1.1 (1.13)	ns
Proximal tubule	111.2 ± 19.2 (2.07)	118.1 ± 23.6 (2.03)	184.9 ± 109.8 (2.21)	S[5]
Distal tubule	39.5 ± 8.0 (1.62)	51.1 ± 24.1 (1.64)	56.7 ± 27.9 (1.72)	ns
Collecting duct	6.2 ± 3.1 (0.78)	8.1 ± 1.7 (0.86)	9.1 ± 6.1 (0.87)	ns
Capillaries	40.7 ± 13.3 (1.63)	64.5 ± 14.5 (1.76)	97.6 ± 81.5 (1.87)	S[1]
Medulla				
Proximal tubule	0.9 ± 2.2 (0.55)	0.01 ± 0.01 (0.98)	0.004 ± 0.01 (0.98)	S[2]
Thin limb of Henle	0.2 ± 0.1 (2.1)	0.04 ± 0.01 (1.84)	0.4 ± 0.8 (1.62)	S[6]
Thick limb of Henle	0.9 ± 0.5 (0.87)	0.3 ± 0.1 (0.72)	5.7 ± 8.7 (1.13)	S[3]
Collecting duct	0.2 ± 0.1 (1.19)	0.1 ± 0.02 (1.18)	2.1 ± 3.4 (1.68)	S[4]
Capillaries	0.4 ± 0.2 (1.47)	0.2 ± 0.1 (1.59)	2.1 ± 3.8 (1.55)	ns

Data in parenthesis are adjusted $\log_{10}$ mean (y) values for regression analyses.
ns = not significant, s = significant.
[1,2] Song, Savannah Sparrow > House Sparrow.
[3–5] Savannah Sparrow > Song, House Sparrow.
[6] House Sparrow > Song, Savannah Sparrow.

ullary interstitium (Nishimura et al., 1989). The osmolality of the fluid in the descending limb of Henle's loop (DLLH) equilibrates with the medullary interstitium by the addition of sodium chloride, with no water addition or abstraction from the tubule fluid (Nishimura et al., 1989). The geometric arrangement of the parallel tubules combined with their transport characteristics must facilitate the functioning of a countercurrent multiplier system. The sodium chloride deposited in the medullary interstitium should facilitate the abstraction of water from the collecting ducts (to concentrate the urine). The lack of water permeability on the part of the DLLH suggests that the fluid in this part of the nephron equilibrates with the medullary interstitium by solute entry only. This enhances sodium chloride delivery to the thick limb of Henle. The anatomical evidence presented in this article supports the physiological interaction of the descending

and ascending limbs of Henle as described by Nishimura et al. (1989).

The anatomical variables that seem to be consistent with the environment the birds inhabit are the percent and volume of the renal medulla. Previous studies have demonstrated that arid zone birds have a higher volume of renal medulla than mesic zone birds (Warui, 1989; Casotti and Richardson, 1992, 1993a; Casotti et al., 1998). In this study, the salt marsh Savannah Sparrow showed the same trend. An animal inhabiting a salt marsh environment might be expected to concentrate its urine more than mesic zone birds (House and Song Sparrows) because of the limited availability of fresh water and the potentially large amount of salt in its diet.

The sizes of the renal corpuscles in the kidneys of the three sparrows were similar to those found in honeyeater birds (Casotti and Richardson, 1993b). This is somewhat surprising as honeyeaters have a predominantly nectar diet that has a high water content (Powers and Nagy, 1988; Weathers and Stiles, 1989). The sparrows examined in this study are predominantly granivorous. It might be expected that animals that filter a larger amount of fluid should possess larger renal corpuscles. This was shown for fresh water fishes, which have larger glomeruli than salt water fishes (Hickman and Trump, 1969).

The proximal tubule was attached directly to the renal corpuscle with no neck segment. This is not unique to sparrows and has been found in other birds (Casotti, 1993; Casotti and Richardson, 1993b). The ultrastructure of the proximal tubules of all sparrow species is suggestive of a marked capacity to reabsorb both water and ions, given the presence of large interdigitations of the basal lamina and numerous mitochondria (Rhodin, 1963; Roberts and Schmidt-Nielsen, 1966). The Savannah Sparrow may have a greater capacity to reabsorb water
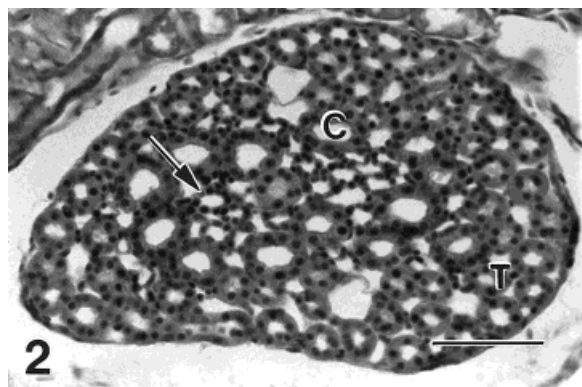

Fig. 2. Light micrograph showing the distribution of nephron tubular elements in cross section through a medullary cone in the House Sparrow, *Passer domesticus*. T, thick limb of Henle; C, collecting duct; arrow, thin limb of Henle. Scale bar = 250 μm.
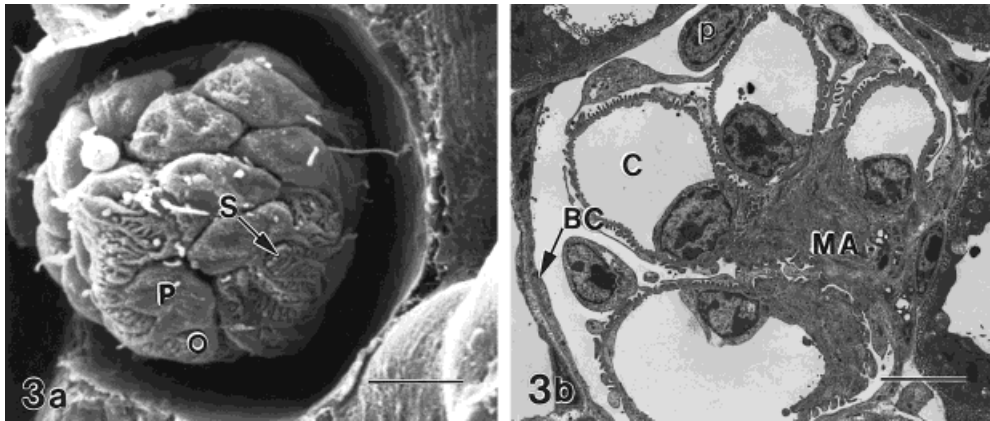
Fig. 3. Scanning (**a**) and (**b**) transmission electron micrograph showing the external structures on the glomerulus of the Song Sparrow, *Melospiza melodia*. P, podocyte; O, primary process (trabeculae); S, secondary process (pedicles); c, capillary; BC, Bowman's capsule; MA, mesangium. Scale bar = 5 μm.

and ions along this portion of the nephron because it has a higher volume and surface area of proximal tubules than do the mesic zone species.

Unlike mammals, where the thin descending limb of Henle consists of different cell types (Barrett et al., 1978a,b; Bachmann and Kriz, 1982), that of sparrows consists of only one cell type. It resembles the type of epithelium found in honeyeater birds and in the early portions of the thin limb of Henle of Gambel's and Japanese quail (Braun and Reimer, 1988; Casotti and Richardson, 1993b). This type of epithelium is typically found in cells that transport solutes passively (Braun and Reimer, 1988). Our data showed that the Savannah and House Sparrows have a significantly higher surface area but not volume of thin limbs of Henle than did the Song Sparrow. This suggests that the thin limb of Henle may be longer in the latter species.

The ultrastructure of the thick limb of Henle in sparrows resembles closely that found in the Desert Quail, *Callipepla gambelii*, with mitochondria occurring between infoldings of a basal labyrinth (Braun and Reimer, 1988). The Savannah Sparrow had a higher surface area of this tubule type compared to the House and Song Sparrows. This type of epithelium is indicative of active transport and, together with the structure of the thin limb of Henle, this morphological pattern fits with the proposed mechanism of producing a concentrated urine in birds, where solutes are transported out of the thick limb and enter passively into the thin limb of Henle (Nishimura et al., 1989).

The Savannah Sparrow has a lower volume of the distal tubule than the mesic zone species; this may be associated with the higher volume of proximal tubule. It suggests that with more functional area at the level of the proximal tubule less of the filtered load remains to be processed by the distal tubule. The ultrastructure of the distal tubule is similar in all species of sparrows examined and resembles closely the morphology seen in previous studies in other birds (Siller, 1971; Nicholson, 1982; Casotti and Richardson, 1993b). Like the thick limb of Henle, the presence of mitochondria and infoldings of the basolateral cell membrane is charac-

teristic of cells involved in active transport. The distal tubules lead into the cortical collecting duct that consists of two cell types, the principal and intercalated cells. The luminal surface morphology of these cell types is the same as those seen in principal and intercalated cells in other birds (Nicholson, 1982; Casotti, 1993; Casotti and Richardson, 1993b). The principal cells reabsorb sodium and the intercalated cells secrete hydrogen ions (but not in exchange for sodium) (Hansen et al., 1978; Evan et al., 1980; Stanton et al., 1984). In addition, the principal cells secrete mucus to prevent uric acid precipitation, thus preventing blockage of the tubule lumen (Guzsal, 1970; Peek and Mc-Millan, 1979).

The sparrow nephron terminates in the medullary collecting duct, and the ultrastructure of this segment is similar to that described for other birds (Siller, 1971; Nicholson, 1982; Casotti and Richardson, 1993b). Its role is reabsorption of water and possibly some sodium from the tubule fluid. The Savannah Sparrow has a significantly higher surface area but not volume of the medullary collecting duct than the mesic zone species, indicating that the collecting duct may be longer, providing a greater opportunity to reabsorb water along this portion of the nephron. In addition, the Savannah Sparrow also has a higher surface area of medullary capillaries, indicating that the capillary network is longer in this species. This may be in concert with the higher surface area of collecting ducts to carry away fluid that is withdrawn from the collecting ducts as they pass through the medullary interstitium.

In summary, this study demonstrates that differences in the anatomy of the kidneys among the sparrows examined are in the amount of medulla, proximal tubule, and distal tubules. No detectable differences were found in the kidney ultrastructure. These data indicate that the salt marsh Savannah Sparrow has the renal morphology necessary to produce a more concentrated urine; however, physiological data in the literature do not indicate that this species has any greater ability to produce a concentrated urine than the mesic zone inhabiting House Sparrow.
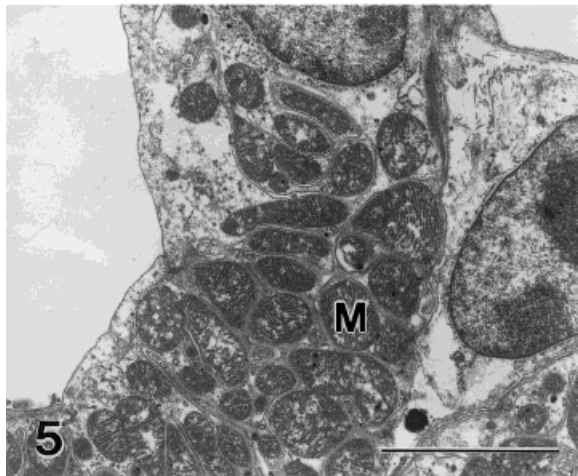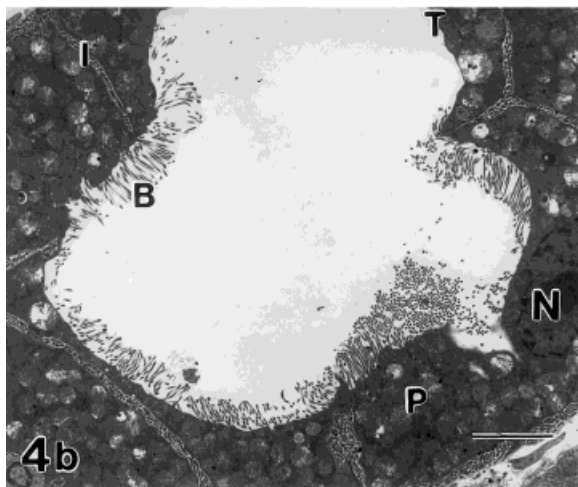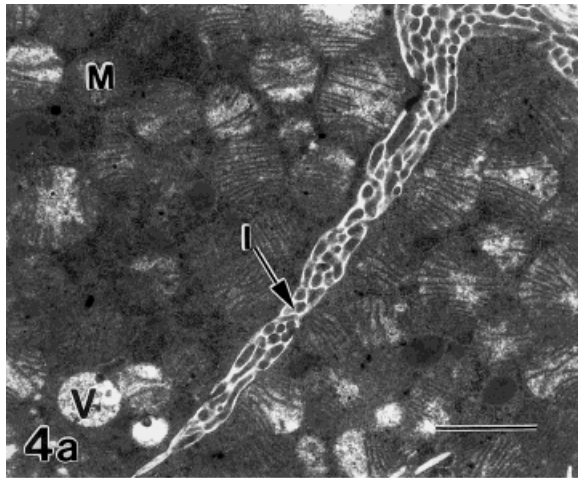
Fig. 4. **a**: Transmission electron micrograph showing intercellular spaces filled with interdigitations in the proximal tubule in the House Sparrow, *Passer domesticus*. **b**: Transmission electron micrograph showing the abrupt transition between the proximal tubule and the thin descending limb of Henle in the House Sparrow, *Passer domesticus*. I, interdigitations; B, brush border; M, mitochondria; N, nucleus; v, condensing vesicles; P, proximal tubule cell; T, thin limb of Henle cell. Scale bar (**a**) = 1 μm; (**b**) = 3 μm.

Fig. 5. Transmission electron micrograph showing the internal structure of the thick ascending limb of Henle in the House Sparrow, *Passer domesticus*. M, mitochondria. Scale bar = 5 μm.
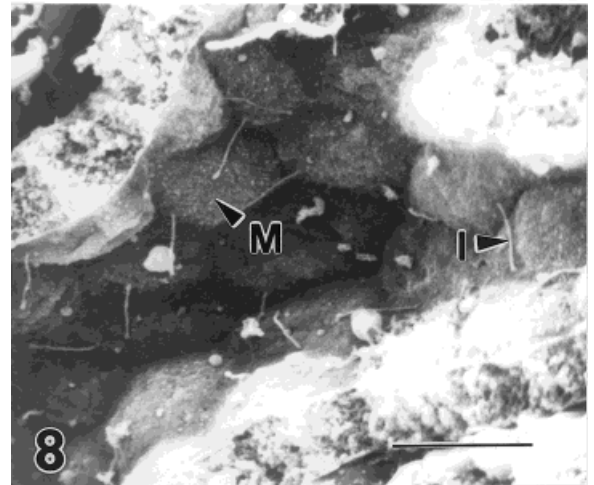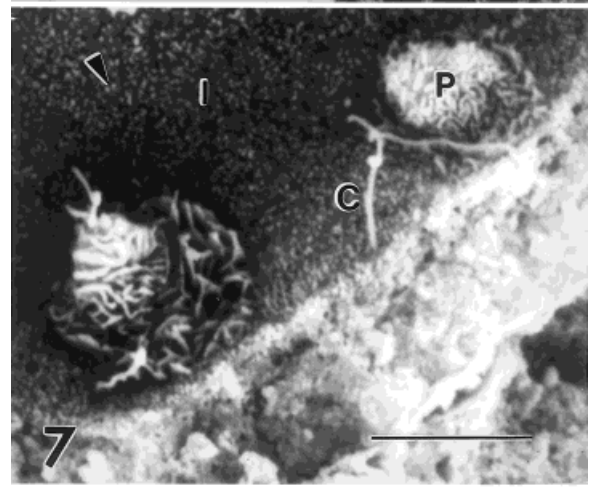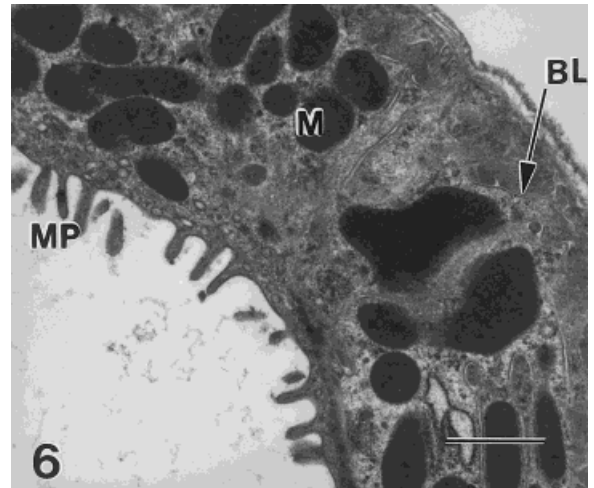
Fig. 6. Transmission electron micrograph showing a distal tubule cell in the Song Sparrow, *Melospiza melodia*. M mitochondria; BL, basal labyrinth; MP, microplicae. Scale bar = 1 μm.

Fig. 7. Scanning electron micrograph showing the surface architecture of the principal and intercalated cells in the cortical collecting duct of the Song Sparrow, *Melospiza melodia*. P, principal cell; I, intercalated cell; C, cilium; arrow, microplicae. Scale bar = 5 μm.

Fig. 8. Scanning electron micrograph showing the surface architecture of the medullary collecting duct cells in the Song Sparrow, *Melospiza melodia*. I, cilium, M, microplicae. Scale bar = 10 μm.

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