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A stereological analysis of kidney structure of honeyeater birds (Meliphagidae) inhabiting either arid or wet environments

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ABSTRACT

Stereology was used to quantify components within the kidney of honeyeater birds. Arid zone and wet zone inhabiting 'matched' body mass pairs of birds were examined. The kidney structure of the arid zone white-fronted honeyeater, *Phylidonyris albifrons* (16.9 g), was compared with that of the wet zone New Holland honeyeater, *Phylidonyris novaehollandiae* (21.9 g), and that of the arid zone spiny-cheeked honeyeater, *Acanthogenys rufogularis* (42.5 g), with that of the wet zone little wattlebird, *Anthochaera lunulata* (62.0 g). Both arid zone honeyeaters had a significantly higher ($P < 0.001$) percentage of medulla in the kidneys, while the wet zone birds had a significantly higher ($P < 0.001$) percentage of cortex. There were few differences between arid and wet zone honeyeaters in the percentage of nephron components in the cortex and medulla. Both arid zone bird species had a significantly larger volume of medulla, a feature characteristic of a high ability to conserve water by producing a concentrated urine. Both wet zone species had a higher volume of cortex but the difference was not significant. Few differences were found in the volumes and surface areas of tubules within the nephron. Differences that did occur were not always consistent with a high ability to conserve either ions or water more efficiently. The volume and surface area of brush border in the proximal tubule were significantly higher in the little wattlebird. This characteristic may lead to a greater capacity of its kidneys to absorb both water and ions.

INTRODUCTION

Studies using DNA–DNA hybridisation techniques have determined that the world's passerines have evolved via 2 radiations: the old endemic Australasian group, the parvorder Corvi, and the parvorder Muscicapae which originated either in Africa or Asia (Sibley & Ahlquist, 1985). Of the Corvi, the honeyeaters (family Meliphagidae) are a group distributed widely throughout Australia as well as the south-western Pacific region, from eastern Indonesia to Palau, the Hawaiian islands and New Zealand (Coates, 1990; Longmore, 1991). Within Australia, some honeyeater species are confined exclusively to wet habitats, while others are restricted to arid zone habitats (Blakers et al. 1984). Birds inhabiting such diverse environments may be subjected to widely differing osmoregulatory demands (Bartholomew & Cade, 1963). Previous studies have shown that some species of honeyeaters which are found exclusively in coastal habitats, have a diet consisting largely of nectar (for review, see Pyke, 1980). In contrast, species inhabiting more arid environments, where the number of nectar producing plants are limited, have a predominantly insectivorous diet (Pyke, 1980; Shurcliff, 1986; Reid, 1990; Longmore, 1991).

Nectar contains relatively large amounts of water and carbohydrate but small quantities of lipids, amino acids and the essential ions, sodium and potassium (Baker & Baker, 1975). Hiebert & Calder (1983) found floral nectar of 26 species of plants to have mean levels of sodium and potassium of 3.4 ± 1.3 and 24.7 ± 5.1 mmol/l respectively. Nicolson & Worswick (1990) found that in 18 species of plants, the mean sodium and potassium concentrations of floral nectar were 9.8 ± 1.4 and 18.7 ± 4.3 mmol/l, respectively. In contrast, insects have high protein and lipid levels as well as a high ionic content while restricted in the amount of water. Mean values reported for the

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concentrations of sodium and potassium in insect haemolymph are 31.5±9.7 and 44.3±4.8 mmol/l (Chapman, 1969), 65±56.8 and 34.9±15.8 mmol/l (Wigglesworth, 1972) and 37.6±1.2 and 25.2±0.7 mmol/l (Nicolson & Worswick, 1990). To accommodate dietary variations in available water and ions, kidney structure may be expected to vary in birds inhabiting two quite different climatic regions. The kidneys of wet zone honeyeaters should be adapted to conserving efficiently the limited quantity of ions available in nectar. Consequently their kidneys should possess a high proportion of cortex and its associated components. Conversely, the kidneys of arid zone honeyeaters should be adapted to water conservation by possessing a high proportion of medulla and its associated components within the kidney (Ambrose & Bradshaw, 1988).

Among vertebrates, the structure of the avian kidney is unique. Unlike the mammalian kidney which has a peripheral cortex and central medulla, the avian kidney is more complex having the medulla arranged as a series of elongated cones intermingled amongst the cortex (Dantzler & Braun, 1980). The apices of the cones converge at the papillary duct and are continuous with the ureter (Braun & Dantzler, 1972). The avian kidney contains both short and long-looped as well as loopless nephrons. The looped nephrons are commonly referred to as mammalian-type and the loopless nephrons as reptilian-type because anatomically they resemble the type of nephrons found in mammals and reptiles respectively (Braun & Dantzler, 1972). Most nephrons in the avian kidney are of the loopless type; for example 90% in the Gambel's quail (*Lophortyx gambelii*), and 68% in the European starling (*Sturnus vulgaris*) (Braun & Dantzler, 1972; Braun, 1978). Unlike mammals, birds are capable of producing only a slightly hyperosmotic urine. Whereas the looped nephrons produce a concentrated urine, their contribution to ureteric urine osmolality is reduced by the greater volumes of dilute urine produced by the loopless nephrons (Braun & Reimer, 1988). Thus even though the urine to plasma osmolality ratio in birds has been found to vary among species, with values ranging from 0.4 in the domestic fowl to 5.8 in the savannah sparrow, the mean value for most birds studied is about 2.0 (Dantzler, 1970; Krag & Skadhauge, 1972; Skadhauge, 1974). These values are considerably lower than those found in mammals where values range from 4.2 in humans to 26.8 in the arid dwelling hopping mouse, *Leggadina hermansburgensis* (Dantzler, 1989; Beuchat, 1990).

In birds, as in mammals, the ability to concentrate urine has been linked to various indices including the length of the loop of Henle, the relative thickness of the renal medulla (Sperber, 1944; Schmidt-Nielsen, & O'Dell, 1961), the percentage medullary thickness (Heisinger & Breitenbach, 1969), and the relative medullary area (Brownfield & Wunder, 1976). These variables are not always consistent in predicting a high renal concentrating capacity (Johnson, 1974; Jamison, 1987; Beuchat, 1990). Recent evidence suggests that in order to produce a concentrated urine, birds require the presence of both short and long-looped nephrons (Jamison, 1987). The reasons for this are unclear, but Layton (1986) suggests that solutes reabsorbed from the ascending limbs of the short-looped nephrons help concentrate fluid in the descending limbs of the long-looped nephrons.

A substantial number of studies have examined the quantitative anatomy of the avian kidney. However, most have examined only the proportion of medulla (Johnson & Mugaas, 1970; Johnson & Ohmart, 1973; Johnson, 1974; Johnson & Skadhauge, 1975) or looped nephrons (Poulson, 1965; Goldstein & Braun, 1986) and found a high positive correlation with renal concentrating ability. Only one previous study on the domestic fowl *Gallus domesticus* (Warui & King, 1985) has examined quantitatively each component constituting the nephron. The present study aimed to investigate quantitatively, differences in the anatomical structure of the kidneys from honeyeaters inhabiting either arid or wet zone environments. Quantitative analysis was carried out using stereological techniques to estimate both volumes and surface area of the kidney and the nephron components.

MATERIALS AND METHODS

Four species of honeyeaters were collected in Western Australia, under licence, using mist nets. The renal anatomy of 'matched' body mass pairs of bird species from wet versus arid zones was examined. Kidneys of the wet zone New Holland honeyeater *Phylidonyris novaehollandiae* (mean body mass 21.9±0.6 g) were compared with those of the arid zone white-fronted honeyeater *Phylidonyris albifrons* (16.9±0.7 g) and those of the wet zone little wattlebird *Anthochaera lunulata* (62.0±4.3 g) with the arid zone spiny-cheeked honeyeater *Acanthagenys rufogularis* (42.5±2.3 g). Eight New Holland honeyeaters and 6 birds of each of the other 3 species were used.

Captured birds were weighed to 0.1 g. They were killed with an intraperitoneal injection of sodium pentobarbitone. Heparin was added to the barbiturate

to prevent blood coagulation. Whole body perfusions were performed by perfusion of half-strength Karnovsky's fixative (1.5% glutaraldehyde, 0.8% paraformaldehyde, 0.066 M phosphate buffer) through the left ventricle. The birds were stored in fixative for 72 h, after which the kidneys were dissected from the body. The length and width of both kidneys were measured using vernier calipers to ± 0.1 mm and the volume of the kidneys estimated by water displacement (Scherle, 1970). For the purpose of this study the anatomy of the left and right kidneys were considered to be identical.

The right kidney was processed routinely for light microscopy. Before embedding, its length and width were measured using vernier calipers. Percentage linear tissue shrinkage ranged between 17 and 28% in the 4 species. A one-way analysis of variance (ANOVA) showed that there was no significant difference in the degree of shrinkage in both the length and the width of the right kidney between species. Following measuring the kidney was embedded in paraffin wax and 10 levels of transverse parallel interrupted serial sections were taken at equal intervals along the length of the kidney. To ensure an unbiased volume estimate the first section was taken at random. Ten levels were used to minimise the coefficient of error of the Cavalieri volume estimate from equations given in Gundersen et al. (1988). At each of the 10 levels, 2 sections were cut to a thickness of 5 μm. One was stained with haematoxylin and eosin and the other with periodic acid-Schiff Alcian blue, the latter being essential to distinguish cortical collecting tubules from distal tubules.

Point counting using the Cavalieri principle outlined in Gundersen et al. (1988) was used to estimate the volumes of the kidney, cortex, medulla and the major blood vessels (i.e. blood vessels larger than capillaries). Similarly the volumes of the cortical and medullary capillaries, glomerulus, proximal tubule, distal tubule, the loop of Henle, cortical and medullary ducts, as well as volumes of the brush border in the proximal tubule, were estimated. The surface areas of the nephron tubules and capillaries were estimated using the formula, $[(V_v/d)\cdot 4]\cdot$reference volume, where V_v is the volume of the component measured from the Cavalieri principle and d is the mean internal diameter of the component measured (Gundersen, 1979). This enabled us to determine whether differences in kidney structure between species were due to the presence of either wider tubules or a greater total length of small tubules.

The left kidney was processed for transmission electron microscopy. The tissue was postfixed in 1% Dalton's osmium tetroxide, washed in a series of graded alcohols, then infiltrated with propylene oxide and embedded in Epon resin. Sections were cut to a thickness of 1 μm then stained with uranyl acetate and lead citrate. After carbon coating, the specimens were viewed in a Philips 301 transmission electron microscope. The surface area of the brush border in the proximal tubule was measured from electron micrographs using the intersection counting technique outlined in Gundersen (1979).

Analysis of covariance (ANCOVA) (Zar, 1984) was used to analyse the data, to correct for variations in both bird body mass when considering the kidney volume, and kidney volume when considering the volume and surface area of nephron components. The tabulated results are presented as the raw mean data ($\pm$S.E.). Statistical analyses were done on the results shown in parentheses in the tables, which represent the $\log_{10}$ adjusted mean (y) values, for the regression lines for each of the species. To compare differences between both slopes and elevations of regression lines, a Student Newman-Keuls test was performed (Zar, 1984). Different independent variables were used in the analysis depending on the anatomical structure of interest. In the case of the volume of the right kidney, the independent variable was bird body mass. For the volumes of the cortex, medulla and major blood vessels, the volume of the kidney served as the independent variable. The volumes and surface areas of the glomeruli, proximal tubules, distal tubules, cortical collecting tubules and cortical capillaries were regressed against the volume of the cortex. The volumes and surface areas of the loops of Henle, collecting ducts and medullary capillaries were regressed against the volume of the medulla. For the volumes and surface areas of the brush border of the proximal tubule, the volume of the proximal tubule was used as the independent variable.

To clarify differences in the kidney structure between species, volume data are also presented in the form of the percentage of components within the kidney, cortex and medulla. As percentages were not adjusted against an independent variable, trends in the level of significance may differ slightly from data presented in the tables. Percentage data were converted to arcsines using the arcsine transformation method (Zar, 1984), and statistical differences analysed using ANOVA.

RESULTS

The percentage volume of renal cortex and medulla differed between the arid zone and wet zone honey-

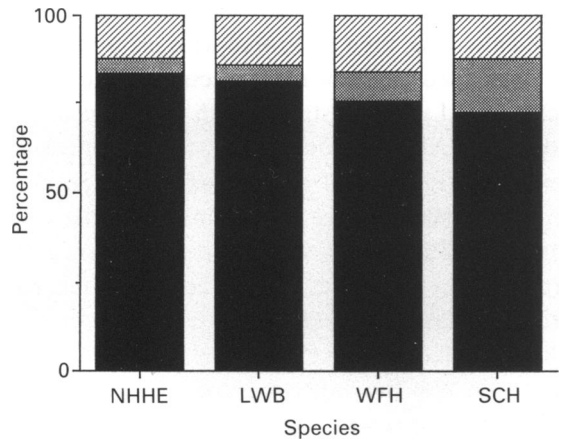

Fig. 1. Percentage volumes of cortex (■), medulla (▩) and major blood vessels (▨) in the kidneys of the New Holland honeyeater (*NHHE*), little wattlebird (*LWB*), white-fronted honeyeater (*WFH*) and spiny-cheeked honeyeater (*SCH*).

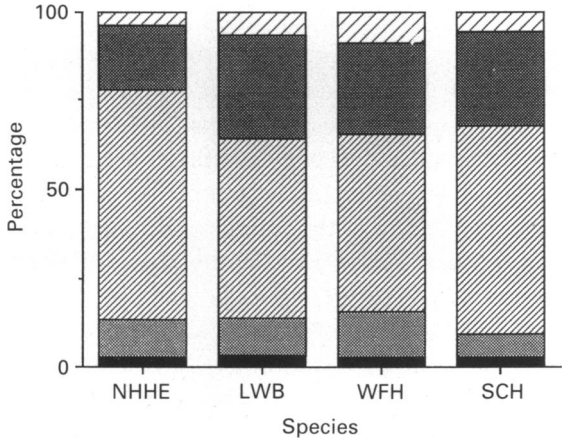

Fig. 2. Percentage volumes of the cortical components: glomerulus, (■), proximal tubule (▨), distal tubule (⊡), collecting tubule (▨) and capillaries (▩) within the kidneys of the New Holland honeyeater (*NHHE*), little wattlebird (*LWB*), white-fronted honeyeater (*WFH*) and spiny-cheeked honeyeater (*SCH*).

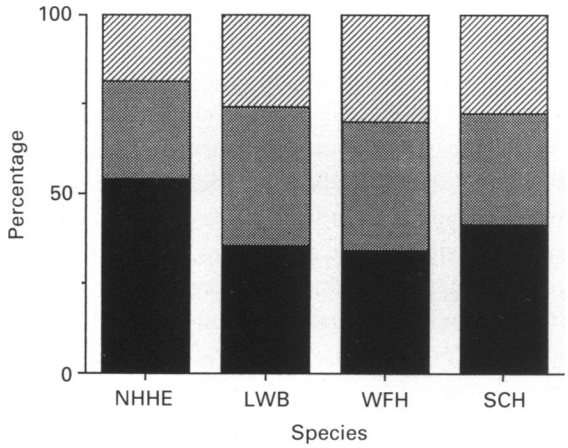

Fig. 3. Percentage volumes of the medullary components: collecting duct, (■), loop of Henle (▩) and capillaries (▨) within the kidneys of the New Holland honeyeater (*NHHE*), little wattlebird (*LWB*), white-fronted honeyeater (*WFH*) and spiny-cheeked honeyeater (*SCH*).

eaters. The kidneys of the spiny-cheeked and white-fronted arid zone honeyeaters contained a significantly higher ($P < 0.001$) percentage of medulla than the honeyeaters found in the wet zones (Fig. 1). Conversely, the 2 species of wet zone honeyeaters had a significantly higher ($P < 0.001$) percentage of cortex than did their arid zone counterparts. The percentage volume of major blood vessels was significantly higher ($P < 0.01$) in the white-fronted honeyeater compared with the New Holland honeyeater (Fig. 1).

In most cases, arid zone and wet zone honeyeaters showed remarkable similarities in the nephron structure. Within the cortex, the volume percentage of glomeruli did not vary greatly between the 4 species (Fig. 2). However, the spiny-cheeked and New Holland honeyeaters were shown to have a significantly higher ($P < 0.01$) percentage of proximal tubule (58.9% and 64.6% respectively), than the little wattlebird and white-fronted honeyeaters (50.9% and 49.7% respectively). The volume percentage of distal tubules was significantly higher ($P < 0.05$) in both the white-fronted honeyeater (9.7%) and little wattlebird (8.5%) than in the spiny-cheeked honeyeater (4.5%). The volume percentage of cortical collecting tubules was significantly higher ($P < 0.05$) in the white-fronted honeyeater (6.6%) than for the New Holland honeyeater (3.1%). The volume percentage of cortical capillaries was similar in most species ranging from 5.3% to 8.8%, except in the New Holland honeyeater, where it was 3.8% (Fig. 2).

Within the medulla, the New Holland honeyeater had a significantly higher ($P < 0.001$) volume percentage (54.1%) of collecting ducts than the other species (Fig. 3). The volume percentage of loops of Henle were significantly higher ($P < 0.001$) in the little wattlebird (38.6%) and white-fronted honeyeater (35.9%). The percentage of the medulla devoted to capillaries was much the same in most species ranging from 25.8 to 30.2%, except in the New Holland honeyeater where the percentage was significantly lower ($P < 0.001$) at 18.8% (Fig. 3).

When comparing the $\log_{10}$ adjusted mean (y) values, both species of arid zone birds had significantly higher volumes of medulla in the kidneys than did the two wet zone species (Table 1). This was significant when comparing the New Holland honeyeater with both arid zone birds ($P < 0.005$) and when comparing the little wattlebird with the spiny-cheeked honeyeater ($P < 0.001$) (Table 1). Both species of wet zone birds had proportionately higher volumes of cortex than did the arid zone honeyeaters but this was not significant.

Of the smaller 'matched' body mass pair, the New Holland honeyeater and white-fronted honeyeater

Table 1. *Mean (± S.E.) volumes of the right kidney and its associated components (mm^3) from 4 species of honeyeater birds. Data in parentheses are adjusted log_{10} mean (y) values for regression analyses*

	Wet		Arid		
Variable	New Holland honeyeater[1]	Little wattlebird[2]	Spiny-cheeked honeyeater[3]	White-fronted honeyeater[4]	*P*
Kidney	98.3±8.0 (1.02)	212.3±13.3 (1.33)	260.3±20.9 (1.37)	88.5±4.6 (1.02)	ns
Cortex	81.8±7.0 (1.10)	162.5±13.2 (1.07)	190.4±19.2 (1.03)	67.1±3.6 (1.06)	ns
Medulla	4.4±0.5 (0.77)	12.3±1.1 (0.88)	38.8±2.7 (1.38)	7.1±0.6 (1.03)	1 vs 3, 4* 2 vs 3**
Major blood vessels	12.1±1.4 (1.18)	37.5±2.6 (1.36)	31.1±2.8 (1.28)	14.3±0.9 (1.34)	ns

* $P < 0.005$, ** $P < 0.001$.

Table 2. *Mean (± S.E.) volumes of components (mm^3) within the nephron and capillaries of the right kidney of 4 species of honeyeater birds. Data in parentheses are adjusted log_{10} mean (y) values for regression analyses*

	Wet		Arid		
Variable	New Holland honeyeater[1]	Little wattlebird[2]	Spiny-cheeked honeyeater[3]	White-fronted honeyeater[4]	*P*
Cortex					
Glomerulus	2.1±0.2 (0.45)	6.3±0.3 (0.56)	5.6±0.6 (0.55)	1.9±0.2 (0.49)	ns
Proximal tubule	52.0±3.7 (0.87)	106.1±8.0 (0.78)	112.8±16.8 (0.84)	33.5±2.3 (0.75)	1 vs 4**
Brush border of proximal tubule	8.2±1.0 (0.90)	25.8±1.2 (1.30)	18.9±2.2 (1.10)	10.0±0.8 (1.20)	2 vs 1, 3*
distal tubule	8.9±1.4 (1.01)	23.8±2.2 (1.21)	11.5±1.2 (0.92)	8.5±0.6 (1.08)	2 vs 3***
Collecting tubule	3.1±0.6 (0.74)	14.0±3.9 (0.58)	10.9±2.2 (0.62)	5.8±0.2 (1.18)	ns
Capillary	15.6±4.3 (1.31)	62.1±8.0 (1.40)	49.6±6.6 (1.38)	17.4±1.3 (1.58)	ns
Medulla					
Loop of Henle	1.2±0.2 (1.41)	4.8±0.5 (1.59)	11.9±1.0 (1.52)	2.5±0.2 (1.55)	ns
Collecting duct	2.3±0.2 (0.70)	4.4±0.5 (0.54)	16.3±1.8 (0.65)	2.4±0.2 (0.52)	1 vs 4**
Capillary	0.9±0.2 (1.42)	3.2±0.4 (1.35)	10.6±0.8 (0.98)	2.2±0.3 (1.56)	ns

* $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$

showed significant differences in the volumes of nephron structures. In the cortex, the New Holland honeyeater had significantly higher ($P < 0.02$) volumes of proximal tubules than did the white-fronted honeyeater. In the medulla, the volume of the collecting ducts was significantly higher ($P < 0.02$) in the New Holland honeyeater than in the white-fronted honeyeater. In 'matched' body mass pair relationships between the larger little wattlebird and spiny-cheeked honeyeater, the volumes of the distal tubules in the cortex were significantly higher ($P < 0.01$) in favour of the little wattlebird. There were no significant differences in the volume of capillaries supplying either the cortex or the medulla (Table 2).

There were few differences in the surface areas of nephron components between 'matched' body mass pairs of species. The only species differences were in the surface areas of the loop of Henle where they were significantly higher ($P < 0.05$) in the white-fronted honeyeater compared to the little wattlebird (Table 3). There were no significant differences between species in the surface areas of glomeruli, proximal tubules,

Table 3. *Mean (± S.E.) surface areas of components (cm^2) within the nephron and capillaries of the right kidney of 4 species of honeyeater birds. Data in parentheses are adjusted log_{10} mean (y) values for regression analyses*

	Wet		Arid		
Variable	New Holland honeyeater[1]	Little wattlebird[2]	Spiny-cheeked honeyeater[3]	White-fronted honeyeater[4]	*P*
Cortex					
Glomerulus	1.0±0.2 (1.15)	2.2±0.2 (1.01)	2.8±0.6 (1.15)	0.9±0.1 (1.23)	ns
Proximal tubule	30.1±5.0 (1.65)	56.3±6.3 (1.41)	77.7±18.1 (1.59)	21.9±1.9 (1.63)	ns
Brush border of proximal tubule	1818±315 (2.30)	5859±454 (2.60)	4025±578 (2.40)	2269±187 (2.50)	2 vs 1, 3*
distal tubule	6.4±1.2 (0.89)	15±2.0 (0.94)	10.0±1.8 (0.79)	6.8±0.6 (1.02)	ns
Collecting tubule	2.1±0.6 (1.49)	7.1±2.1 (1.32)	8.3±2.0 (1.51)	3.5±0.3 (1.91)	ns
Capillary	18.5±5.9 (1.21)	68.2±10.6 (1.69)	15.3±1.9 (1.71)	15.4±1.6 (1.29)	ns
Medulla					
Loop of Henle	0.05±0.01 (1.4)	0.2±0.03 (1.09)	69.7±10.6 (1.33)	0.2±0.03 (1.52)	2 vs 4*
Collecting duct	0.04±0.01 (0.79)	0.07±0.01 (0.90)	1.3±0.3 (2.48)	0.1±0.01 (0.84)	ns
Capillary	0.05±0.02 (0.60)	0.2±0.03 (1.19)	2.1±0.3 (2.27)	0.2±0.03 (1.21)	slope significant

* $P < 0.05$

distal tubules, cortical collecting tubules, medullary collecting ducts, or in the cortical capillaries. It was not possible to assign a significance level to the medullary capillaries, as the slope of the regression lines differed ($P < 0.02$) between species (Table 3).

Examination of the ultrastructure of the proximal tubule revealed that the little wattlebird had both significantly higher volumes ($P < 0.05$) and surface areas ($P < 0.05$) of brush border than did the New Holland honeyeater and the spiny-cheeked honeyeater (Tables 2, 3).

DISCUSSION

There have been few studies undertaken to examine quantitively the structure of the avian kidney. This is the first stereological study of passerine bird species in the parvorder Corvidae, examining the avian kidney anatomy from species in a single family (Meliphagidae). Previous studies have concentrated on the domestic fowl, order Galliformes (Warui & King, 1985) or examining birds over several orders encompassing the parvorder Muscicapae radiation (Warui, 1989).

Honeyeaters have varied diets, feeding on various combinations of nectar, insects and fruits, depending on the species of bird (Pyke, 1980). Honeyeaters inhabiting wet environments tend towards nectarivory, while those inhabiting arid environments tend to feed on insects. This study found that 2 arid zone species, the white-fronted and spiny-cheeked honeyeaters, had significantly higher volumes of medulla in the kidney than did the New Holland honeyeater and little wattlebird, both wet zone species. Warui (1989), studying the arid dwelling zebra finch (*Poephila guttata*) and common starling (*Sturnus vulgaris*), found similar results. Earlier quantitative studies undertaken by dissection have found that arid dwelling birds have a well developed renal medulla (Johnson & Mugaas, 1970; Johnson & Ohmart, 1973; Johnson & Skadhauge, 1975; Goldstein & Braun, 1986). The present study is one of the few studies to confirm these findings using stereology. At a broad level within the kidney, this study found that the percentage of cortex was higher in birds inhabiting a wet environment. Similar results have been found for the mesic inhabiting white-rumped munia (*Lonchura striata*), the collared turtle dove (*Streptopelia decaocta*) and several species of aquatic birds (Warui, 1989).

We found fewer anatomical differences than expected in the nephron components of arid versus wet zone honeyeaters. Not all cortical components had significantly larger volumes and/or surface areas from birds inhabiting one climatic zone. The New Holland honeyeater was shown to have significantly higher

volumes of proximal tubules than did the white-fronted honeyeater. In mammals, approximately 70% of all ions are reabsorbed in the proximal tubule, while in birds only 50–60% glomerular filtered sodium and potassium are reabsorbed at this level (Laverty & Dantzler, 1982). New Holland honeyeaters have the anatomical potential to reabsorb a higher proportion of filtered ions at this level than do the white-fronted honeyeaters. The majority of remaining ions are reabsorbed in the distal tubule (Guyton, 1981; Dantzler, 1989). The little wattlebird had a significantly higher volume of distal tubules than did its 'matched' body weight pair, the spiny-cheeked honeyeater. As with the proximal tubule, this indicates a greater potential for ion uptake along this region of the nephron in the little wattlebird.

Although both species of arid zone honeyeaters were shown to have a higher volume of medulla than both species of wet zone honeyeaters, the same was not true of all the components within the medulla. In mammals, generally, longer loops of Henle are associated with a high urine concentrating ability (Sperber, 1944; Schmidt-Nielsen & O'Dell, 1961). This study found that the white-fronted honeyeater had a significantly higher surface area of the loops of Henle than did the little wattlebird. As there was no significant difference in the volume of the loop of Henle between the 2 species, this indicated that the loops of Henle in the arid zone white-fronted honeyeater were longer than in the little wattlebird. With regard to the collecting ducts, the New Holland honeyeater had a significantly higher volume than did the white-fronted honeyeater. Given that the loop of Henle and collecting ducts are the second major areas of water reabsorption after the proximal tubule (Dantzler, 1989), we expected these components to have a consistently greater volume and/or surface area in the arid zone honeyeaters, but this proved not to be the case.

If honeyeaters from one environment have a high urine concentrating capacity, this may result from quantitative variations in the nephron tubule ultrastructure. In the ultrastructure of the proximal tubule, the little wattlebird contained both a higher volume and surface area of brush border than did the New Holland honeyeater and spiny-cheeked honeyeater. In the small intestine of vertebrates, the epithelium is lined by numerous microvilli whose primary function is to increase the surface area for greater absorption of luminal fluid (Yamamoto, 1988; Holmes & Lobley, 1989). Likewise an increase in the volume and surface area of brush border may lead to a greater quantity of glomerular filtrate being reabsorbed in the proximal tubule. As the other wet zone honeyeater, however, the New Holland honeyeater had the least amount of brush border, the ability to absorb ions might not be a function of the habitat type.

The kidney anatomy of honeyeaters inhabiting arid environments shows that they have the nephron structure to produce a highly concentrated urine. Honeyeaters from wetter areas have kidneys which may be able to conserve ions more effectively but the results remain inconclusive. Physiological experiments to examine the renal concentrating ability in these birds may give a better understanding of the honeyeater kidney adaptability to varying climatic zones and dietary regimes.

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