

Comparison of renal and salt gland function in three species of wild ducks

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Summary

Three processes central to osmoregulation of marine birds were compared in three species of ducks that differ in habitat affinity, diet and saline tolerance. These processes are filtration of Na^+ and water from the plasma by the kidneys, their reabsorption along the renal tubules, and secretion by the salt glands. Barrow's goldeneyes *Bucephala islandica*, the most marine species, have the highest rates for all three processes and only this species can secrete all the infused salt *via* the salt glands. Rates of all three processes are lower in mallards *Anas platyrhynchos*, the most freshwater species. Following saline acclimation, mallards could excrete all the infused Na^+ by a combined Na^+ excretion of the kidneys and salt glands. Canvasbacks *Aythya valisineria*, despite being

more saline tolerant than mallards, are unable to excrete all the infused Na^+ . They produce a large volume of urine (like mallards) that has a low $[\text{Na}^+]$ (like goldeneyes). Salt gland secretion Na^+ concentration did not differ among the three species, but only goldeneyes secrete at a rate sufficient to eliminate all infused Na^+ *via* the salt glands. Differences in saline tolerance of these ducks species cannot be fully explained by differences in their filtration, reabsorption and secretion of Na^+ and water, suggesting that the intestinal tract plays an important role.

Key words: osmoregulation, kidney, salt gland, mallard, *Anas platyrhynchos*, canvasback, *Aythya valisineria*, Barrow's goldeneye, *Bucephala islandica*.

Introduction

All marine birds have salt glands that, together with the kidneys, maintain body fluid homeostasis, despite the excess sodium chloride (NaCl) they ingest. They have similar total body water, but twice the daily water flux of birds that lack salt glands (Hughes et al., 1987; Nagy and Peterson, 1988). Among species that produce highly concentrated salt gland secretion (SGS), the salinity of the drinking water has no effect on drinking rate (Harriman, 1967; Walter and Hughes, 1978; Bennett et al., 2003). Such birds become dehydrated only when they drink water more concentrated than their SGS (Bennett et al., 2003).

Three processes central to osmoregulation in marine birds are filtration of sodium (Na^+) and water from the plasma by the kidneys, reabsorption of filtered water and Na^+ by cells along the renal tubules, and secretion of Na^+ by the salt glands. These processes must have evolved simultaneously to adapt to the osmoregulatory requirements of birds that use habitats of widely disparate salinities, ranging from freshwater to full-strength seawater. Renal filtration of marine birds is unaffected by either acclimation to saline or acute saline loading and almost all the filtered Na^+ (and water) is reabsorbed along the renal tubules, regardless of plasma $[\text{Na}^+]$ (Hughes, 1995). The reabsorbed Na^+ can be secreted by the salt glands in less water than was imbibed with it. The concentration and rate of salt gland secretion determines the amount of osmotically free

water it can generate for the birds' other physiological processes (Schmidt-Nielsen, 1960).

Many species of ducks switch seasonally between freshwater and saline habitats. When the drinking water of Pekin ducks is changed from freshwater to saline, their salt glands hypertrophy, enhancing their capacity to excrete salt (Schmidt-Nielsen and Kim, 1964), but the glomerular filtration rate (GFR) is little affected (Holmes et al., 1968) and the fractional reabsorption of Na^+ is reduced (Holmes et al., 1968; Hughes et al., 1989). Whether these responses occur in wild ducks has not been reported.

Therefore, in this study, we compared simultaneous kidney and salt gland function in three species of ducks: freshwater mallards (tribe *Anatini*, *Anas platyrhynchos*), estuarine canvasbacks (tribe *Aythiini*, *Aythya valisineria*) and marine Barrow's goldeneyes (tribe *Mergini*, *Bucephala islandica*). Goldeneyes, the most saline-tolerant, have larger kidney mass (Kališnińska et al., 1999; D. C. Bennett and M. R. Hughes, unpublished data) and extracellular fluid volume (Bennett, 2002) than mallards, the least saline-tolerant species. Canvasbacks have large kidneys like the goldeneyes (D. C. Bennett and M. R. Hughes, unpublished data), but a smaller extracellular fluid volume, like the mallards (Bennett, 2002). Water flux rates of all three species (Bennett, 2002) are roughly twice the rate predicted allometrically for seabirds (Hughes et

Table 1. *Glomerular filtration rate (GFR) and effective renal plasma flow (ERPF) of birds with and without salt glands in relation to habitat type and diet*

Species	Mass (g)	GFR (ml min ⁻¹)	ERPF (ml min ⁻¹)	Habitat	Diet	Source
Without salt glands:						
Order Struithioniformes						
<i>Dromaius novaehollandiae</i>	40700	16.2		TA	O	1
Order Galliformes						
<i>Alectoris chukar</i>	511.7	0.58		TA	O	2
<i>Coturnix chinensis</i>	51.4	0.55	1.50	TM	O	3
<i>Coturnix pectoralis</i>	107.3	0.68	4.07	TA	H	3
<i>Coturnix japonica</i>	122.3	1.55		TM	H	4
<i>Gallus gallus var. dom.</i>	1890	4.13	32.32	TM	O	5–33
<i>Meleagris pavo</i>	7400	5.68		TM	H	34, 35
<i>Callipepla gambelii</i>	158.4	0.23		TA	H	36–42
Order Psittaciformes						
<i>Melopsittacus undulatus</i>	37.5	0.14		TA	O	43
<i>Cacatua roseicapilla</i>	335.9	0.79	3.76	TA	O	44
Order Trochiliformes						
<i>Calypta anna</i>	5.1	0.04		TM	N	45
Order Columbiformes						
<i>Zenaidura macroura</i>	119	0.27	2.05	TM	H	46
<i>Columbia livia</i>	569.3	4.04		TM	H	47
Order Falconiformes						
<i>Falco sparverius</i>	126.0	0.27		TM	C	48
Order Passeriformes						
<i>Anthochaera carunculata</i>	99	0.35		TM	N	49
<i>Sturnus vulgaris</i>	77.1	0.50	4.27	TM	O	50–57
<i>Nectarinia osea</i>	5.8	0.03		TM	N	58
<i>Passer domesticus</i>	22.8	0.13		TM	H	59
<i>Melospiza melodia</i>	18.4	0.13		TM	O	60
With salt glands:						
Order Anseriformes						
<i>Branta canadensis</i>	3670	6.24		FW	H	61
<i>Anas platyrhynchos</i>	983	2.70	11.00	FW	O	61–63
<i>Anas platyrhynchos var. dom.</i>	2513	7.44	52.85	FW	O	64–72
<i>Aythya valisineria</i>	1052	2.27	5.23	FW	O	62
<i>Bucephala islandica</i>	767	4.06	10.63	MR	C	62
Order Charadriiformes						
<i>Larus argentatus</i>	1000	4.40		MR	C	73
<i>Larus dominicanus</i>	905	3.09		MR	C	74
<i>Larus glaucescens</i>	900	3.84	13.61	MR	C	61, 75–77

TA, terrestrial arid; TM, terrestrial mesic; FW, freshwater; MR, marine; H, herbivore; O, omnivore; N, nectivore; C, carnivore.

Source: ¹Dawson et al. (1991), ²Goldstein (1990), ³Roberts et al. (1985), ⁴Roberts and Hughes (1983), ⁵Berger et al. (1960), ⁶Dantzler (1966), ⁷Glahn et al. (1988a,b), ⁸Gregg and Wideman (1990), ⁹Hyden and Knutson (1959), ¹⁰Korr (1939), ¹¹Leary et al. (1998), ¹²Nechay and Nechay (1959), ¹³Orloff and Davidson (1959), ¹⁴Pitts (1938), ¹⁵Pitts and Korr (1938), ¹⁶Radin et al. (1993), ¹⁷Roberts (1991a), ¹⁸Roberts (1992), ¹⁹Sanner (1965), ²⁰Shannon (1938a,b), ²¹Shideman et al. (1981), ²²Singh and Battacharyya (1983), ²³Skadhauge (1964), ²⁴Skadhauge and Schmidt-Nielson (1967), ²⁵Sperber (1960), ²⁶Svendsen and Skadhauge (1976), ²⁷Sykes (1960a,b), ²⁸Vena et al. (1990), ²⁹Wideman and Gregg (1988), ³⁰Wideman and Laverty (1986), ³¹Wideman and Nissley (1992), ³²Wideman and Satnick (1989), ³³Wideman et al. (1987), ³⁴Palmore et al. (1981), ³⁵Vogel et al. (1965), ³⁶Anderson (1980), ³⁷Braun (1976), ³⁸Braun and Dantzler (1972), ³⁹Braun and Dantzler (1974), ⁴⁰Braun and Dantzler (1975), ⁴¹Williams and Braun (1996), ⁴²Williams et al. (1991), ⁴³Krag and Skadhauge (1972), ⁴⁴Roberts (1991b), ⁴⁵S. Medler (unpublished data), ⁴⁶Shoemaker (1967), ⁴⁷Chan et al. (1972), ⁴⁸Lyons and Goldstein (2002), ⁴⁹Goldstein and Bradshaw (1998b), ⁵⁰Braun (1978), ⁵¹Clark and Wideman (1980), ⁵²Laverty and Dantzler (1982), ⁵³Laverty and Dantzler (1983), ⁵⁴Laverty and Wideman (1989), ⁵⁵Roberts and Dantzler (1989), ⁵⁶Roberts and Dantzler (1992), ⁵⁷Wideman et al. (1980), ⁵⁸T. J. McWhorter (unpublished data), ⁵⁹Goldstein and Braun (1988), ⁶⁰Goldstein and Rothschild (1993), ⁶¹Hughes (1980), ⁶²This study, ⁶³Hughes et al. (1999), ⁶⁴Bennett et al. (2000), ⁶⁵Bradley and Holmes (1971), ⁶⁶Gerstberger et al. (1985), ⁶⁷Holmes and Adams (1963), ⁶⁸Holmes et al. (1968), ⁶⁹Hughes et al. (1989), ⁷⁰Schutz et al. (1992), ⁷¹Simon and Gray (1991), ⁷²Thomas and Phillips (1975), ⁷³Douglas (1966), ⁷⁴Gray and Erasmus (1988), ⁷⁵Hughes (1995), ⁷⁶Hughes et al. (1993), ⁷⁷Raveendran (1987).

al., 1987; Nagy and Peterson, 1988). We hypothesize that (1) neither saline acclimation nor acute saline loading affect GFR in any of the three species, and (2) saline tolerance is determined by the efficiency of renal tubular reabsorption of water and Na^+ , and secretion of Na^+ by the salt glands.

Materials and methods

Animals

24 adult ducks (eight mallards, *Anas platyrhynchos* L., eight Canvasbacks, *Aythya valisineria* Gray, and eight Barrow's goldeneyes, *Bucephala islandica* Gmelin) were held in large partially covered outdoor enclosures at the University of British Columbia Animal Care Facility. Groups included equal numbers of males and females. Water was presented in 70 liter plastic wading pools and completely replenished twice daily. Half the ducks of each species drank freshwater, while the other half drank 300 mmol l^{-1} NaCl. They ate duck pellets (17% protein, 2750 kcal kg^{-1} ; Buckerfield's, Abbotsfield, BC, Canada) containing 12.7% water and 68, 145 and $190 \text{ mmol l}^{-1} \text{ kg}^{-1}$ Na^+ , K^+ and Cl^- , respectively.

Experiments

These experiments followed the guidelines set forth by the Canadian Council on Animal Care. Each duck was fasted overnight and weighed. Venous catheters were placed in the left and right tibiotarsal veins (for infusion of saline and markers and for blood sampling, respectively) and were kept patent with heparinized isotonic saline. The duck's wings were lightly bound to the body with Velcro straps and the bird was placed on a foam-lined restrainer. The duck's head projected into a large funnel that directed SGS into preweighed glass vials. The SGS of poor secretors was collected by capillary tube. A cannula inserted into the cloaca diverted ureteral urine into a preweighed plastic tube.

An initial 1 ml blood sample was taken and the duck was given a priming injection of 37 kBq of ^{14}C -inulin (marker for GFR) and 370 kBq of ^3H -para-aminohippuric acid (^3H -PAH; marker for effective renal plasma flow, ERPF). An infusion of 75 mmol l^{-1} NaCl, containing 0.15 kBq ml^{-1} of ^{14}C -inulin and 1.1 kBq ml^{-1} of ^3H -PAH, was begun ($0.175 \text{ ml min}^{-1}$). After a 1 h equilibration period, four 10–15 min urine samples

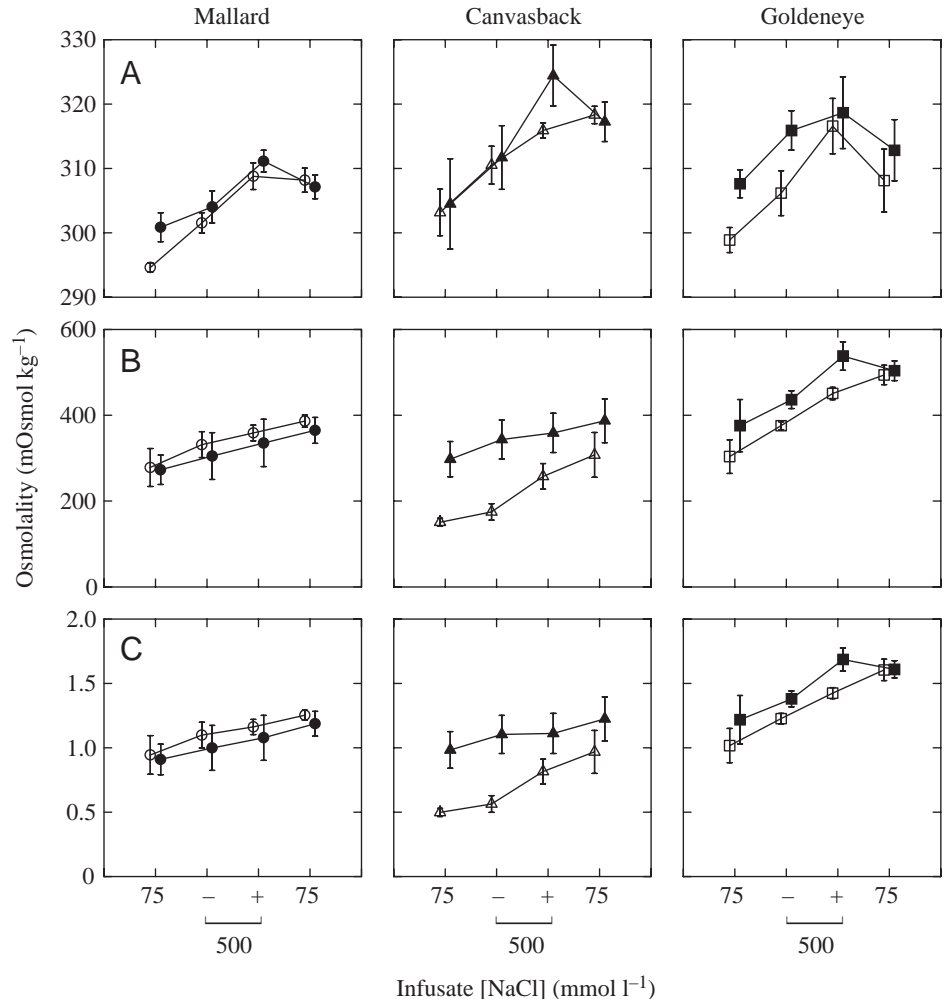


Fig. 1. Effect of hypotonic and hypertonic saline infusion (75 and 500 mmol l^{-1} NaCl, respectively) on (A) plasma and (B) urine osmolality and (C) their ratio (Urine:Plasma) in freshwater (open symbols) and saline-acclimated (filled symbols) in mallards *Anas platyrhynchos* (circles), canvasbacks *Aythya valisineria* (triangles) and Barrow's goldeneyes *Bucephala islandica* (squares). The period of 500 mmol l^{-1} NaCl infusion was subdivided into two parts: the period prior to secretion (–) and the period of secretion (+). Values are means \pm S.E.M. ($N=4$ ducks per treatment).

were collected. Then infusate NaCl concentration was increased to 500 mmol l^{-1} and urine was collected at 10–20 min intervals until the duck began to secrete. Four simultaneous 10–20 min collections of urine and SGS were made. Finally, infusate NaCl concentration was reduced to 75 mmol l^{-1} and three simultaneous 10–20 min collections of urine and SGS were made. Urine and SGS volumes were determined by weighing their tubes before and after the collection period. A blood sample (0.4 ml) was taken at the mid-point of each collection period.

Blood, urine and SGS samples were centrifuged for 3 min at $15\,600 \text{ g}$ and the supernatant fluids were transferred into 1.5 ml centrifuge tubes and stored at -20°C until assayed. Plasma, urine and infusate ^3H and ^{14}C concentrations were determined using a Beckman LS 6500 liquid scintillation counter (Fullerton CA, USA). Determinations of $[\text{Na}^+]$ and

[K⁺] of plasma, urine and SGS were made by cesium internal standard flame photometry (Model 943, Instrumentation Laboratory S.p.A, Milano, Italy); and osmolality (Osm) of the plasma and urine by vapor pressure osmometry (Model 5500; Wescor Inc., Logan UT, USA). Subscripts pl, u and sgs designate plasma, urine and salt gland secretion, respectively.

Calculations and statistics

All calculations are as described in Pitts (1968) and Goldstein (1993). GFR and ERPF were calculated as:

$$\text{GFR} = [\text{inulin}]_{\text{u}}\text{UFR} / [\text{inulin}]_{\text{pl}}$$

and

$$\text{ERPF} = [\text{PAH}]_{\text{u}}\text{UFR} / [\text{PAH}]_{\text{pl}},$$

where [marker]_u and [marker]_{pl} are the marker (inulin or PAH) concentrations in the urine and plasma, respectively, and UFR

is the urine flow rate. Fractional reabsorption of water (FR_{H₂O}) was calculated as:

$$\text{FR}_{\text{H}_2\text{O}} = (1 - [\text{inulin}]_{\text{pl}} / [\text{inulin}]_{\text{u}}) \times 100$$

and fractional reabsorption of Na⁺ and K⁺ (FR_{Na} and FR_K, respectively) was calculated as:

$$\text{FR}_{\text{ion}} = (\text{GFR}[\text{ion}]_{\text{pl}} - \text{UFR}[\text{ion}]_{\text{u}}) / \text{GFR}[\text{ion}]_{\text{pl}},$$

where [ion]_{pl} and [ion]_u represent the Na⁺ and K⁺ concentrations of the plasma and urine, respectively.

All analyses and calculations were made on each sample collected and were, within individuals, averaged for each infusate, so that each infusate period for an individual duck is represented by a single value. The 500 mmol l⁻¹ NaCl infusion was divided into two periods: prior to secretion and active secretion. Data are reported as means ± standard errors (S.E.M.)

and statistically analyzed using SYSTAT 9 for Windows (SPSS Science, Chicago, IL, USA). Differences among species and infusion periods and between treatments and sexes were assessed by repeated-measures analysis of variance (ANOVA). Significance is claimed at *P*<0.05, although higher *P* values suggesting trends are also reported. Relationships among variables were examined using correlation and stepwise linear regression.

To examine the relationships of GFR to habitat and diet of birds, we collected GFR data on 27 species of adult non-dehydrated birds, disregarding the methods used to measure GFR (Table 1). Data were obtained from original sources whenever possible. For each species we calculated a single data point that is the mean of all reported values. GFR was standardized by regressing it on body mass, after log₁₀-log₁₀ transformation, and analysing the residuals by ANOVA.

Results

Plasma composition

Overall, Osm_{pl}, [Na]_{pl} and [K]_{pl} varied significantly among species and infusion periods, but not between the treatments or sexes. Mallards had a lower Osm_{pl} (*P*<0.06; Fig. 1) and [Na]_{pl} (*P*<0.002; Fig. 2) and a higher [K]_{pl} (*P*<0.002; Fig. 3) than both canvasbacks and goldeneyes. Infusion of hypertonic saline significantly

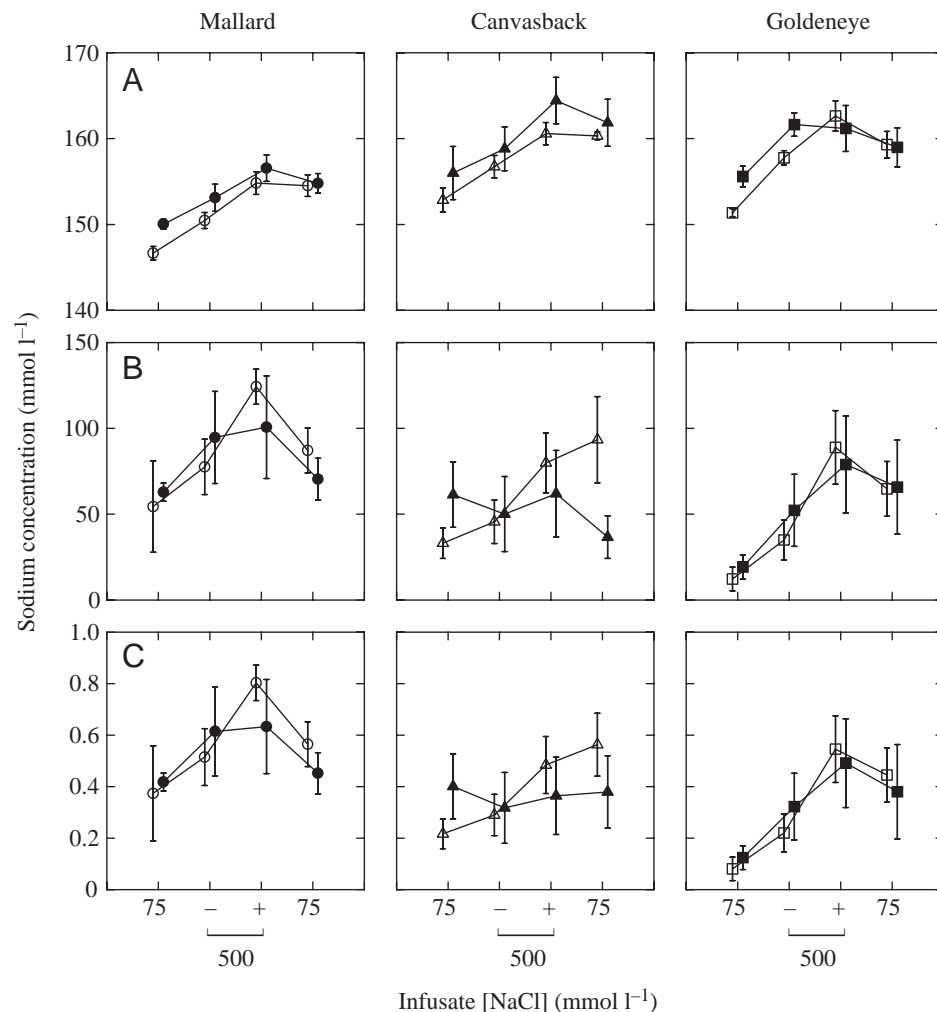


Fig. 2. Effect of hypotonic and hypertonic saline infusion (75 and 500 mmol l⁻¹ NaCl, respectively) on (A) plasma and (B) urine sodium concentration and (C) their ratio (Urine:Plasma) in freshwater (open symbols) and saline-acclimated (filled symbols) mallards *Anas platyrhynchos* (circles), canvasbacks *Aythya valisineria* (triangles) and Barrow's goldeneyes *Bucephala islandica* (squares). The period of 500 mmol l⁻¹ NaCl infusion was subdivided into two parts: the period prior to secretion (-) and the period of secretion (+). Values are means ± S.E.M. (*N*=4 ducks per treatment).

increased Osm_{pl} , $[\text{Na}]_{\text{pl}}$ and $[\text{K}]_{\text{pl}}$ in all three species and these remained high during active salt secretion. Osm_{pl} and $[\text{Na}]_{\text{pl}}$, but not $[\text{K}]_{\text{pl}}$, decreased after the infusion of hypotonic 75 mmol l⁻¹ NaCl was reinstated.

Kidney function

GFR was significantly greater in goldeneyes than in either mallards or canvasbacks ($P < 0.005$) and differed between freshwater and saline-acclimated ducks only in canvasbacks (Fig. 4), due mainly to lower GFR in freshwater females. GFR did not vary among the infusion periods in any species ($P > 0.5$). ERPF was significantly lower in canvasbacks than in either mallards or goldeneyes ($P < 0.008$). When ducks were infused with hypertonic saline, ERPF increased only in mallards ($P < 0.03$; Fig. 4). Neither saline acclimation nor sex affected ERPF.

Fractional reabsorption of water and Na⁺ varied significantly among the three species ($P < 0.02$ and $P < 0.0004$, respectively; Fig. 5). They were highest in goldeneyes, lowest in canvasbacks and intermediate in mallards (Fig. 5). Fractional reabsorption of water and Na⁺ of mallards was not affected by saline acclimation, sex or infusate concentration, but both tended to be higher in saline-acclimated canvasbacks ($P < 0.08$ and $P < 0.01$, respectively), due almost exclusively to the low values of one freshwater female. In goldeneyes, fractional reabsorption of water increased ($P < 0.005$) and reabsorption of Na⁺ decreased ($P < 0.002$) with infusion period (Fig. 5). Fractional reabsorption of K⁺ did not differ among or within species, except that it was significantly lower in freshwater mallards during the final infusion of 75 mmol l⁻¹ NaCl (Fig. 5). Goldeneyes had lower UFR than either mallards or canvasbacks ($P < 0.01$). UFR was affected by saline only in canvasbacks, and was lower in saline-acclimated ducks ($P = 0.04$) and reduced by saline infusion in freshwater ducks ($P < 0.01$; Fig. 4).

Overall, Osm_{u} (Fig. 1) and $[\text{K}]_{\text{u}}$ (Fig. 3), but not $[\text{Na}]_{\text{u}}$ (Fig. 2), varied among species ($P = 0.0007$, $P = 0.0005$ and $P = 0.14$, respectively). Goldeneyes had the highest Osm_{u} and $[\text{K}]_{\text{u}}$ and, together with canvasbacks, the lowest $[\text{Na}]_{\text{u}}$. Canvasbacks also have the lowest Osm_{u} and $[\text{K}]_{\text{u}}$. Osm_{u} ,

$[\text{Na}]_{\text{u}}$ and $[\text{K}]_{\text{u}}$ varied significantly among infusion periods (all $P < 0.00001$; Figs 1–3), but only Osm_{u} varied between treatments ($P = 0.04$), due primarily to lower Osm_{u} of freshwater canvasbacks (Fig. 1). During hypertonic saline infusion, all three species significantly increased Osm_{u} and it remained high during active salt secretion. $[\text{Na}]_{\text{u}}$ and $[\text{K}]_{\text{u}}$ increased in mallards and goldeneyes regardless of their drinking water regime. In canvasbacks, only freshwater ducks increased $[\text{Na}]_{\text{u}}$ and none increased $[\text{K}]_{\text{u}}$.

Urine flow rate is correlated to both GFR and fractional reabsorption of water ($\text{FR}_{\text{H}_2\text{O}}$) in all three species (Fig. 6). UFR and GFR were positively correlated in mallards and goldeneyes, but not in canvasbacks (Fig. 6). Stepwise linear regression indicated that UFR of mallards and goldeneyes was predicted by a combination of both GFR and $\text{FR}_{\text{H}_2\text{O}}$:

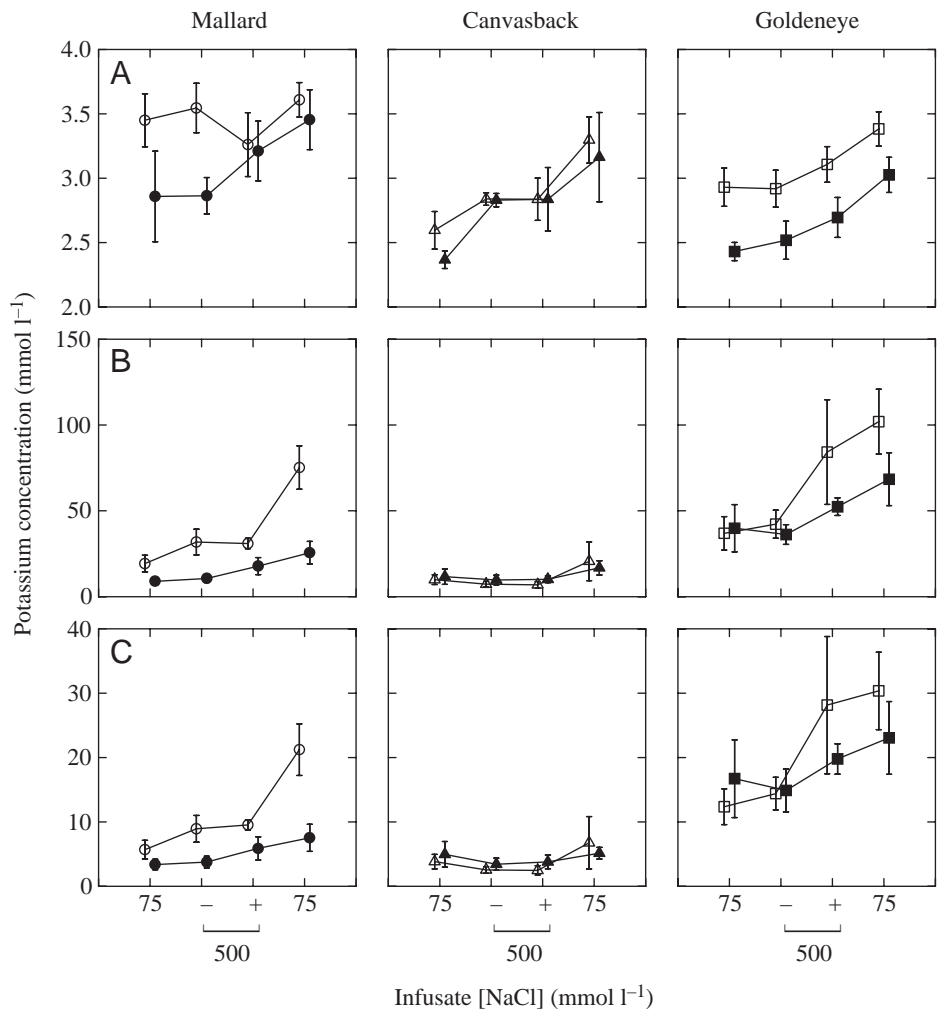


Fig. 3. Effect of hypotonic and hypertonic saline infusion (75 and 500 mmol l⁻¹ NaCl, respectively) on (A) plasma and (B) urine potassium concentration and (C) their ratio (Urine:Plasma) in freshwater (open symbols) and saline-acclimated (filled symbols) mallards *Anas platyrhynchos* (circles), canvasbacks *Aythya valisineria* (triangles) and Barrow's goldeneyes *Bucephala islandica* (squares). The period of 500 mmol l⁻¹ NaCl infusion was subdivided into two parts: the period prior to secretion (-) and the period of secretion (+). Values are means \pm S.E.M. ($N = 4$ ducks per treatment).

$$\text{Mallards: UFR} = 2.0 + (0.039 \times \text{GFR}) - (0.021 \times \text{FR}_{\text{H}_2\text{O}}),$$

$$r = 0.83, P < 0.0001,$$

$$\text{Goldeneyes: UFR} = 3.6 + (0.012 \times \text{GFR}) - (0.036 \times \text{FR}_{\text{H}_2\text{O}}),$$

$$r = 0.95, P < 0.0001,$$

and could be similarly predicted in canvasbacks if one freshwater female were excluded:

$$\text{Canvasbacks: UFR} = 1.6 + (0.021 \times \text{GFR}) - (0.016 \times \text{FR}_{\text{H}_2\text{O}}),$$

$$r = 0.81, P < 0.0001,$$

otherwise UFR of canvasbacks was predicted solely by $\text{FR}_{\text{H}_2\text{O}}$.

Salt gland function

The time required to initiate secretion did not vary among the species ($P=0.12$) nor was it affected by treatment ($P=0.89$) or sex ($P=0.35$). It required 59.3 ± 3.8 min ($N=24$ ducks) of

infusion (500 mmol l^{-1} NaCl at $0.175 \text{ ml min}^{-1}$) to initiate secretion. Freshwater mallards and one freshwater female canvasback produced only a trace of SGS. $[\text{Na}^+]_{\text{sgs}}$ did not vary among the species ($P=0.56$) or between the sexes ($P=0.23$). Saline acclimation increased $[\text{Na}^+]_{\text{sgs}}$ of mallards and goldeneyes ($P=0.04$ and $P=0.01$, respectively), but not of canvasbacks ($P=0.25$; Fig. 7). Salt gland secretion rate varied among species ($P=0.0003$; goldeneyes>mallards>canvasbacks) and was increased by saline acclimation only in mallards (Fig. 7).

Discussion

Kidneys and salt glands of marine birds act interactively to maintain the volume and composition of body fluids within some homeostatically controlled range. The salt glands secrete excess NaCl as a hypertonic fluid and are the primary site of Na^+ excretion, while the kidneys rid the body of excess water, nitrogenous wastes and other osmolytes. To this end, kidneys of marine birds should maintain a high GFR and a high tubular reabsorption of Na^+ and water. Therefore, secretion of excess NaCl directly reflects renal Na^+ filtration and reabsorption. This study simultaneously compared the filtration and reabsorption of Na^+ and water from the kidneys, and secretion of Na^+ by the salt glands in three species of ducks of utilize habitats of different salinities.

Kidney function

Saline acclimation and acute saline loading have little effect on GFR of ducks (Holmes et al., 1968; Hughes, 1980; Hughes et al., 1989, 1999; Fig. 4) or other species with salt glands (Douglas, 1966; Hughes, 1995). GFR of goldeneyes is roughly twice that of mallards, canvasbacks and Pekin ducks (Table 1, Fig. 4), but is similar to that of other marine birds (gulls; Douglas, 1966; Hughes, 1980, 1995; Hughes et al., 1993). The Canada goose *Branta canadensis*, the most terrestrial of the anseriforms studied to date, has the lowest GFR (Hughes, 1980). This suggests that birds well adapted to highly saline water have higher GFR, and that GFR may vary among habitat types. We examined the generality of this relationship by comparing GFR of 27 species of adult birds for which data are available (Table 1). GFR varied

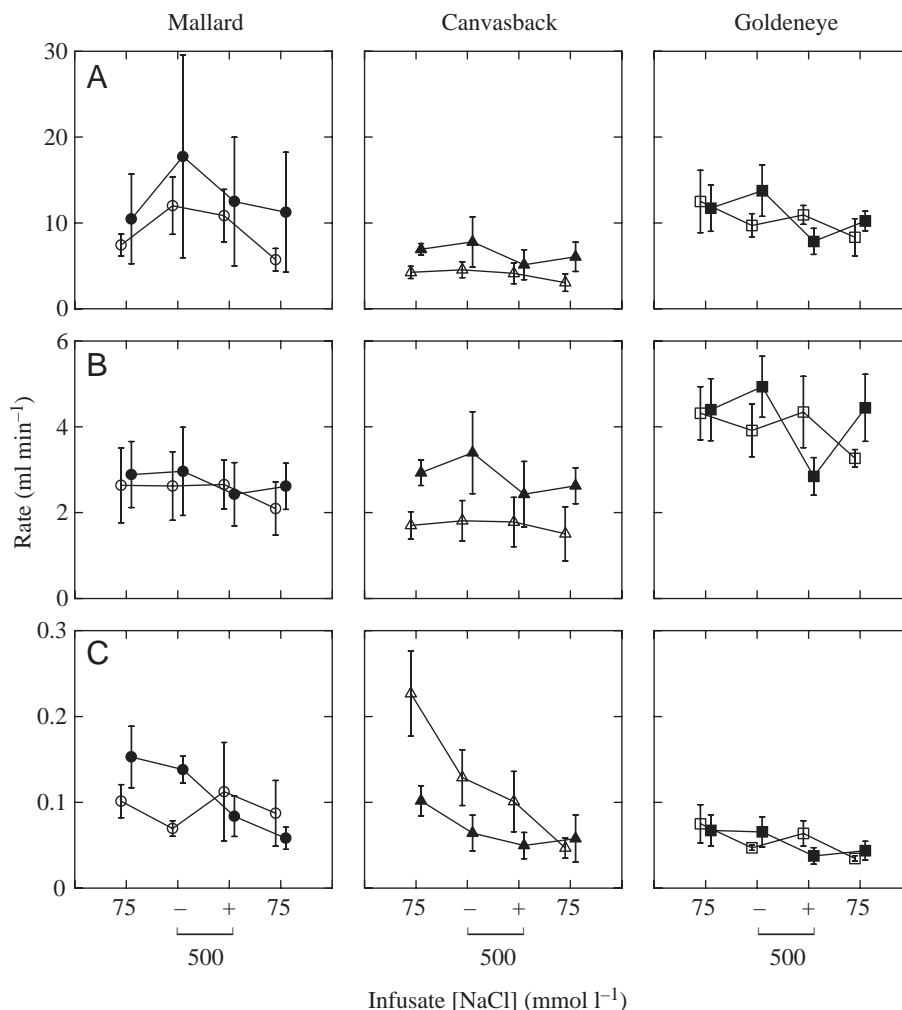


Fig. 4. Effect of hypotonic and hypertonic saline infusion (75 and 500 mmol l^{-1} NaCl, respectively) on (A) effective renal plasma flow (ERPF), (B) glomerular flow rate (GFR) and (C) urine flow rate (UFR) in freshwater (open symbols) and saline-acclimated (filled symbols) mallards *Anas platyrhynchos* (circles), canvasbacks *Aythya valisineria* (triangles) and Barrow's goldeneyes *Bucephala islandica* (squares). The period of 500 mmol l^{-1} NaCl infusion was subdivided into two parts: the period prior to secretion (−) and the period of secretion (+). Values are means \pm S.E.M. ($N=4$ ducks per treatment).

significantly among birds from different habitat types ($P=0.02$; Figs 8, 9). Marine species had a significantly higher GFR ($P=0.02$) and terrestrial arid species had a significantly lower GFR ($P=0.05$) than species from either terrestrial mesic or freshwater habitats, which did not differ significantly from each other ($P=0.9$).

Yokota et al. (1985) identified the need to eliminate water loads and metabolic wastes as the major factors that tend to increase GFR among vertebrates. The results of the preceding analysis support this hypothesis. The high GFR of marine birds is consistent with their larger kidneys (Hughes, 1970; Kalisińska et al., 1999), greater water flux (Hughes et al., 1987; Nagy and Peterson, 1988; Bennett, 2002) and Na^+ flux (Goldstein and Bradshaw, 1998a; Goldstein, 2002) and larger extracellular fluid volumes (Bennett, 2002).

Marine birds are carnivorous and should presumably excrete large amounts of urates. Whether these patterns reflect adaptations to a marine environment and/or effects of a carnivorous diet have not yet been examined. Only one terrestrial avian carnivore, the American kestrel *Falco sparverius*, has been studied and it has a low GFR (Lyons and Goldstein, 2002; Table 1) and small kidneys, like other birds that lack salt glands (Hughes, 1970). We found no relationship between diet and GFR, standardized to body mass ($P=0.58$; Table 1). Large renal mass and a high rate of body fluid filtration appear to be adaptations to the saline environment. Studies on terrestrial avian carnivores, including Falconiform birds that have salt glands (Cade and Greenwald, 1966), might clarify these relationships.

Goldeneyes, the most marine of the three duck species, have the highest fractional reabsorption of water and Na^+ (Fig. 5), thus a low UFR (Fig. 4) and $[\text{Na}^+]_u$ (Fig. 2). They significantly increased the fractional reabsorption of water and decreased the fractional reabsorption of Na^+ when infused with hypertonic saline (Fig. 5), as did gulls (Hughes, 1995). In contrast, mallards had a lower fractional reabsorption of water and Na^+ (Fig. 5) and produced a greater volume of urine (Fig. 4) that had a higher $[\text{Na}^+]_u$ (Fig. 2). Although canvasbacks produced a large volume of urine like mallards (Fig. 4), they had a low $[\text{Na}^+]_u$ like goldeneyes (Fig. 2). Saline infusion did not affect fractional reabsorption of water and Na^+ in mallards and canvasbacks (Fig. 5).

Birds can adjust UFR by two mechanisms: they may vary the rate of fluid delivery to the renal tubules (GFR) and/or adjust tubular water reabsorption. Neither GFR nor fractional water reabsorption of the three species of wild ducks were much affected by saline acclimation or by acute saline loading (Figs 4, 5). With the exception of female freshwater canvasbacks, both mechanisms regulated urine flow of ducks equally well (Fig. 6). Chickens (Wideman, 1988), red wattlebirds *Anthochaera carunculata* (Goldstein and Bradshaw, 1998b) and kestrels (Lyons and Goldstein, 2002) also use both mechanisms to adjust urine flow. Fractional reabsorption of water is considered the more important regulator of urine flow in wattlebirds (Goldstein and Bradshaw, 1998b) and probably Chukars *Alectoris chukar* (Goldstein, 1990).

ERPF of mallards and goldeneyes (Fig. 4) is similar to ERPF of gulls (Raveendran, 1987) and galahs (Roberts, 1991b), but

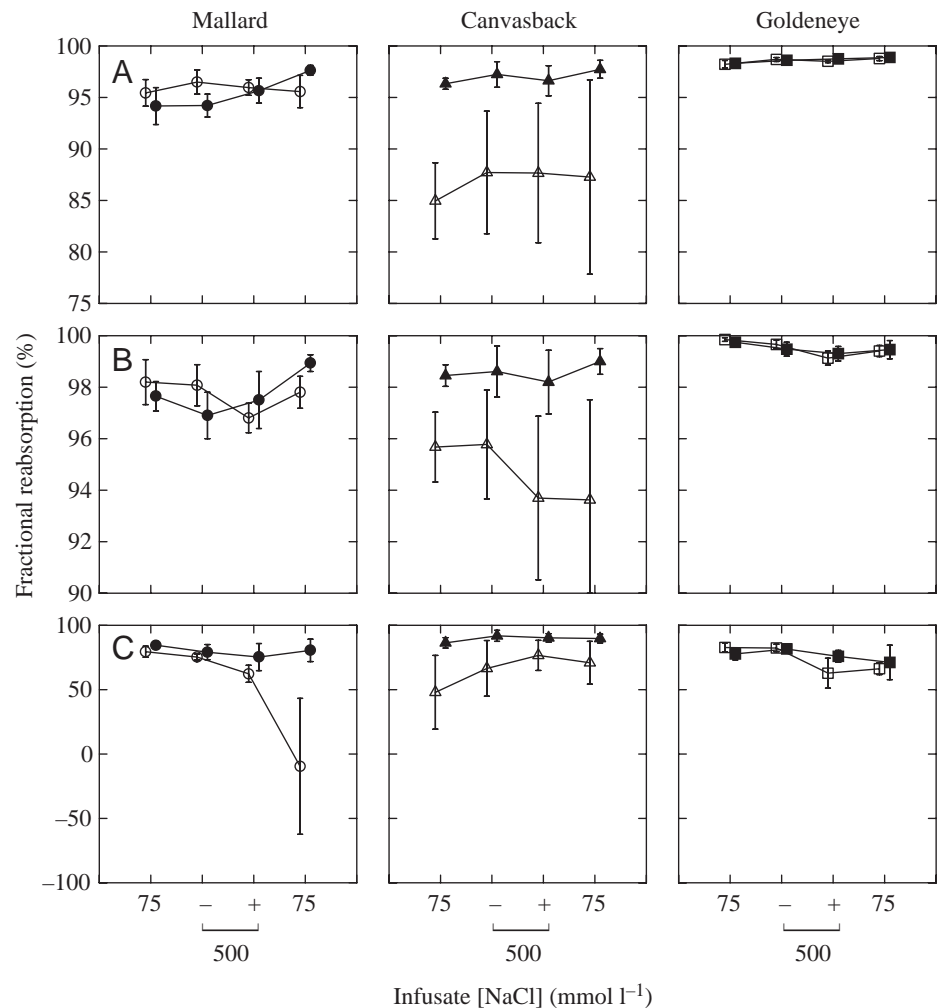


Fig. 5. Effect of hypotonic and hypertonic saline infusion (75 and 500 mmol l^{-1} NaCl , respectively) on the fractional reabsorption of (A) water, (B) sodium and (C) potassium in freshwater (open symbols) and saline-acclimated (filled symbols) mallards *Anas platyrhynchos* (circles), canvasbacks *Aythya valisineria* (triangles) and Barrow's goldeneyes *Bucephala islandica* (squares). The period of 500 mmol l^{-1} NaCl infusion was subdivided into two parts: the period prior to secretion (-) and the period of secretion (+). Values are means \pm S.E.M. ($N=4$ ducks per treatment).

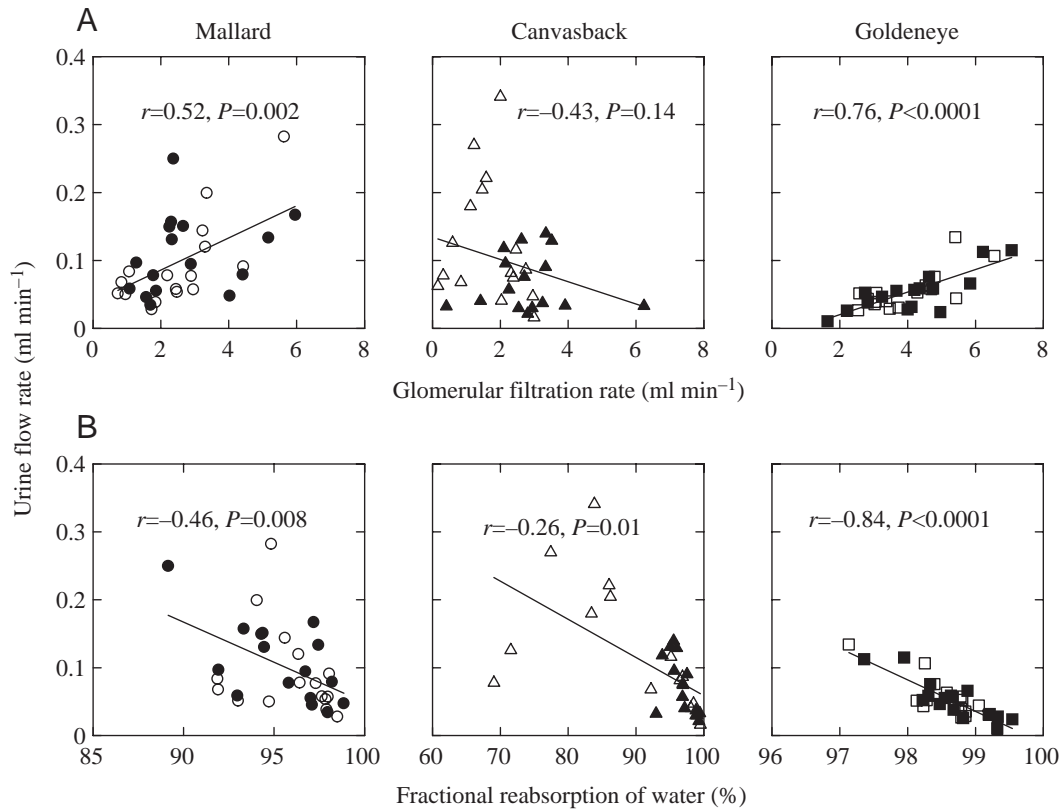


Fig. 6. Relationship between urine flow rate and (A) glomerular filtration rate and (B) the fractional reabsorption of water in freshwater (open symbols) and saline-acclimated (filled symbols) mallards *Anas platyrhynchos* (circles), canvasbacks *Aythya valisineria* (triangles) and Barrow's goldeneyes *Bucephala islandica* (squares).

lower than that of Pekin ducks, chickens and quail (Table 1). Canvasbacks (Fig. 4) have the lowest ERPF of any avian species studied, while domesticated varieties of birds (chicken and Pekin duck) have the highest ERPF (Table 1). We found no relationship between ERPF (Table 1), standardized to body mass (Fig. 8), and habitat ($P=0.92$; Fig. 9). Species differences in ERPF do not suggest any significant pattern, as other attributes of avian osmoregulation, such as water flux, extracellular fluid volume and kidney size, appear to do.

Salt gland function

$[Na^+]_{SGS}$, of saline infused ducks, did not differ among the three species, and was higher following saline acclimation only in mallards and goldeneyes (Fig. 7). Salt gland secretion rate did differ among the three species and was highest in goldeneyes (Fig. 7). Only goldeneyes secreted all the infused Na^+ via their salt glands. Goldeneyes were able to drink 550 mmol l⁻¹ NaCl without changing water intake, yet never secreted when handled during saline acclimation (Bennett, 2002). Saline-acclimated mallards did excrete all infused Na^+ , but incorporated renal excretion to do so. Canvasbacks were unable to excrete all the infused Na^+ . At salinities above 225 mmol l⁻¹

NaCl, mallards decreased water flux (drinking), but canvasbacks tolerated 450 mmol l⁻¹ NaCl with no change in water flux (Bennett, 2002). The SGS of saline infused canvasbacks is more concentrated than their drinking water, yet is produced at a low rate (Fig. 7). Their limited extrarenal Na^+ excretion, together with their low renal Na^+ excretion (Fig. 2), suggest they should be unable to eliminate all the Na^+ they ingested (Bennett, 2002). Nevertheless, they tolerated

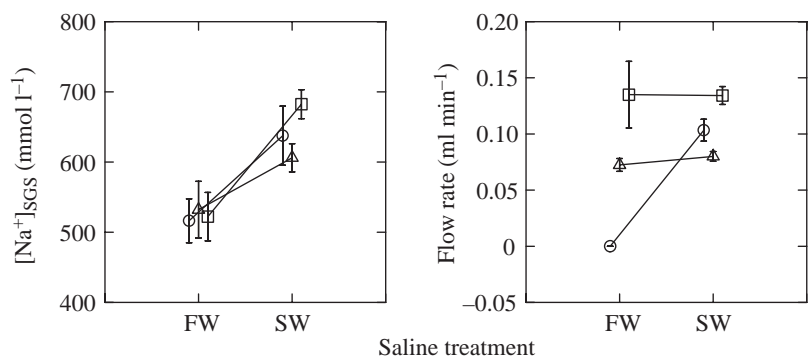


Fig. 7. Salt gland secretion $[Na^+]$ and flow rate in freshwater (open symbols) and saline-acclimated (filled symbols) mallards *Anas platyrhynchos* (circles), canvasbacks *Aythya valisineria* (triangles) and Barrow's goldeneyes *Bucephala islandica* (squares) infused intravenously with 500 mmol l⁻¹ NaCl at 0.175 ml min⁻¹. Values are means ± S.E.M. ($N=4$ ducks per treatment).

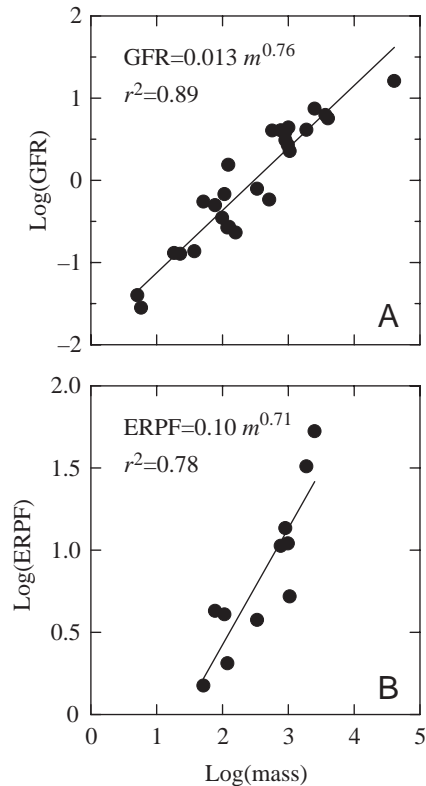


Fig. 8. (A) Glomerular filtration rate (GFR) and (B) effective renal plasma flow (ERPF) as a function of body mass (m) in birds. Data and sources are given in Table 1.

450 mmol l⁻¹ NaCl (Bennett, 2002). How they did so, despite their apparently limited ability to excrete Na⁺, remains unresolved, but may involve water and Na⁺ transport by the anterior and posterior segments of the intestinal tract.

This paradox could be satisfied if the gut did not absorb all the ingested Na⁺. There is some evidence that this may be so. Pekin ducks drink approximately 225 ml kg⁻¹ day⁻¹ (Fletcher and Holmes 1968; Bennett et al., 2003). If they drink 300 mmol l⁻¹ NaCl, their estimated Na⁺ flux would be 67.5 mmol l⁻¹ kg⁻¹ day⁻¹, but Na⁺ flux measured by ²²Na turnover was only 21.4 mmol l⁻¹ kg⁻¹ day⁻¹ (Roberts and Hughes, 1984). We are currently examining Na⁺ balance in the three species of ducks used in this study.

Many species of birds modify their urine in the lower intestinal tract to conserve water and/or Na⁺. For example, water and Na⁺ excretion rates of chickens (Skadhauge, 1968) and quail (Anderson and Braun, 1985) are higher in ureteral urine than in voided urine (cloacal fluid). Schmidt-Nielson et al. (1963) suggested that birds with salt glands might reabsorb Na⁺ and water from the urine in the lower intestinal tract. By secreting the reabsorbed Na⁺ extrarenally in less water than was absorbed with it, they could generate osmotically free water. Postrenal modification of urine has the potential to play an important osmoregulatory role in ducks. Pekin ducks (Hughes and Raveendran, 1994) and mallards (Hughes et al., 1999) reflux urine into their hindgut. Mallards reflux about

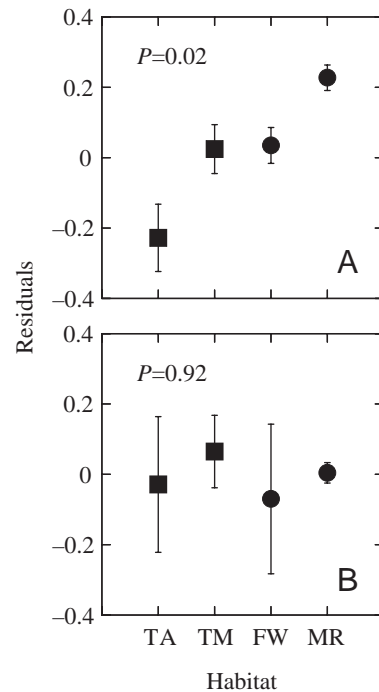


Fig. 9. Comparison of (A) glomerular filtration rate (GFR) and (B) effective renal plasma flow (ERPF) of birds in relation to habitat type (TA, terrestrial arid; TM, terrestrial mesic; FW, freshwater; MR, marine). Data are calculated from residuals of logGFR or logERPF on log(body mass) (Fig. 8; raw data and sources are given in Table 1) and are expressed as mean residual values \pm S.E.M.

20% of their urine, regardless of drinking water salinity (Hughes et al., 1999). The capacity for Na⁺ uptake in the hindgut of Pekin ducks is only slightly diminished by saline acclimation (Skadhauge et al., 1984), and their cloacal fluid (Hughes et al., 1992) is more concentrated than their urine (Hughes et al., 2003). Postrenal modification of urine may help explain the inconsistencies in osmoregulatory responses of canvasback ducks.

Morphology

It is interesting to speculate on the morphological basis for the differences in kidney and salt gland function observed in this study. The larger kidneys and GFR of goldeneyes, and marine birds in general, presumably reflect an increased number of glomeruli. But whether the higher fractional reabsorption of water and Na⁺ (Fig. 5) and urine-concentrating capacity (Fig. 1) is due to a higher proportion of mammalian-type nephrons and fewer reptilian-type nephrons is not known. The proportion of kidney mass composed of medullary cones is high in marine species (Goldstein and Braun, 1989; Goldstein, 1993), which presumably reflects a high proportion of mammalian-type nephrons. Wideman and Nissley (1992) found that domestic chickens that thrived on saline drinking water had higher ratios of mammalian-type to reptilian-type nephron as compared to those that lost body mass.

Staaland (1967) examined the anatomical basis for

variations in salt gland function in Charadriiform birds. He found that the SGS concentration was correlated with the length of the secretory tubule. Although SGS rate was not measured in that study, Staaland (1967) suggested that salt gland size, and presumably the number of lobules, determines SGS flow rate. Given that we found SGS flow rate and not $[Na^+]_{SGS}$ differed among the three species measured in this study (Fig. 7), it could be argued that goldeneyes have relatively larger salt glands, containing more lobules, than either mallards or canvasbacks, but all three species have similar lobular anatomy (secretory tubule length).

Conclusions

We hypothesized that (1) neither saline acclimation nor acute saline loading affect GFR in any of the three species, and (2) saline tolerance is determined by the efficiency of renal tubular reabsorption of water and Na^+ , and secretion of Na^+ by the salt glands. The results support both hypotheses. Goldeneyes, the most marine species, had the highest rates of filtration (GFR), fractional reabsorption of water and Na^+ , and salt gland Na^+ excretion and were the only species that secreted all the infused Na^+ via the salt glands. Rates of these processes were all lower in mallards, the most freshwater species. However, the high volume and Na^+ concentration of urine of saline-acclimated mallards, coupled with extrarenal Na^+ secretion, eliminated all the infused Na^+ . If mallards infused with 500 mmol l^{-1} NaCl can excrete all infused Na^+ , why can they not drink greater than 300 mmol l^{-1} NaCl? In contrast, canvasbacks were unable to excrete all the infused Na^+ , yet tolerated higher drinking water salinities than mallards (Bennett, 2002). This suggests that osmoregulation of canvasbacks involves levels of Na^+ and water regulation by organs other than the kidneys and the salt glands. It may be that the intestinal tract plays an important role in conservation of water in canvasbacks.

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